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SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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Volume 84

Number 2

NEW YORK
BOTANICAL GARDEN





Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

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Date of this issue 7 August 1985

The Spiral Trace Fossil *Gyrolithes* de Saporta, 1884 in the Pliocene Tirabuzon Formation Near Santa Rosalia, Baja California Sur, Mexico

Edward C. Wilson

Abstract.—The spiral trace fossil *Gyrolithes* de Saporta, 1884 in the Pliocene Tirabuzon Formation near Santa Rosalia, Baja California Sur, Mexico, by Edward C. Wilson. *Bull. Southern California Acad. Sci.*, 84(2):57-66, 1985. The largest recorded specimens of the enigmatic spiral trace fossil *Gyrolithes* are abundant in the Pliocene Tirabuzon Formation near Santa Rosalia, Baja California Sur, Mexico. They grade gradually into *Thalassinoides*-type burrows. Both types of burrows are lined by scratch marks, suggesting excavation by a decapod crustacean. Associated mollusks indicate a depth of 55 to 90 m.

In March, 1975, S. P. Applegate, now of the Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Mexico City, introduced me briefly to the Pliocene *Gyrolithes* that crop out strikingly at Loma del Tirabuzon northwest of Santa Rosalia, Baja California Sur, Mexico. At the invitation of the Instituto, I returned to the locality in February 1979, measured a section, and spent eight days examining, photographing, and selectively collecting these trace fossils. This paper and an earlier abstract (Wilson 1981) disclose the results of that work.

Occurrence

Loma del Tirabuzon is an informal name applied by Applegate (1978, p. 56) to a 0.6 km long, flat-topped cliff and associated badlands on the shores of the Gulf of California 2.3 road miles (3.7 km) to 2.7 road miles (4.3 km) north and northwest along Mexico Highway 1 from the intersection of the highway with the main street entering Santa Rosalia, Baja California Sur, Mexico (Fig. 1). It lies between the mouths of Arroyo del Purgatorio and Arroyo de la Soledad. The highway runs between the base of the cliff and the narrow beach. The km post marked "4 km" is beside the highway near the northwest end of the exposure (1979).

Loma del Tirabuzon is formed in the Pliocene Tirabuzon Formation (Carreno 1982, a replacement name for the preoccupied Gloria Formation of Wilson 1948). The formation may be divided here into three major units (Figs. 2, 3A). The lowest unit is a cliff-forming sandstone containing shells of pectens, oysters, epitoniids, barnacles, echinoid spines, and *Gyrolithes*. This unit is 27.5 m thick at the southeast end of the cliff where the section was measured but thickens considerably northwestward as progressively lower beds are exposed by the southeast dip of the section. Unconformably overlying it is a 0.6 to 0.9 m thick silty sandstone that contains numerous marine mammal bones, shark teeth, mollusk casts, and the entrances to the *Gyrolithes* burrow systems. A slope-forming shale with small marine bivalve casts overlies the silty sandstone. The shale unit is 23 m thick at the southeast end of the cliff but thins northwestward and is absent at

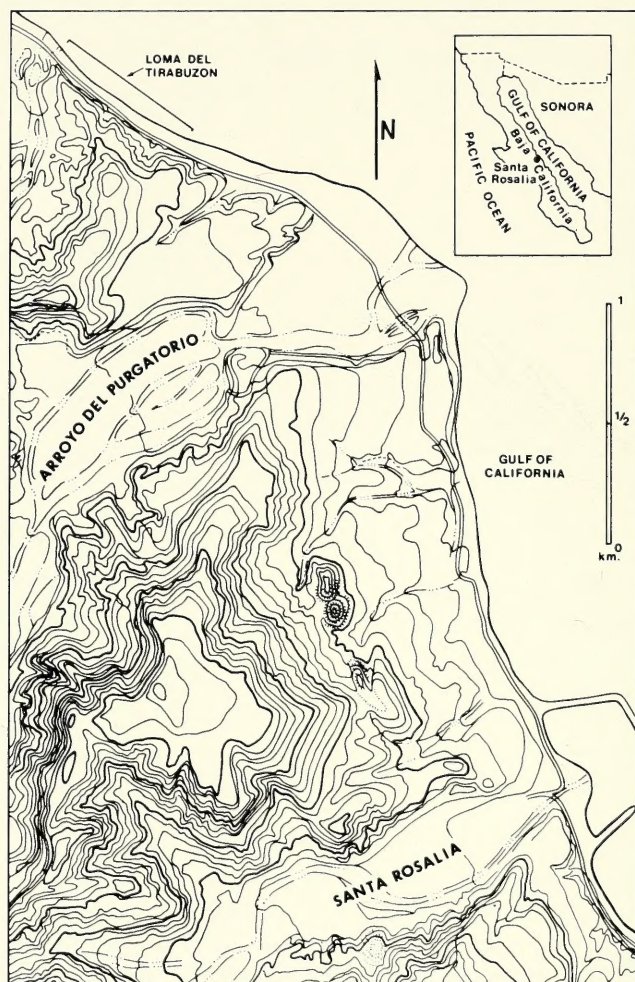


Fig. 1. Index map showing location of Loma del Tirabuzon on Baja California Sur coast northwest of Santa Rosalia. Contour interval 10 m. Modified from Wilson and Rocha (1955).

the extreme northwest end of the cliff due to the dip of the section and to the disconformity at its top. A 2.5 m thick, horizontal, Pleistocene marine terrace composed of boulders and cobbles, with sparse mollusks, disconformably overlies the Tirabuzon Formation and is capped by a thin soil.

The upper ends of the *Gyrolithes* burrow systems are generally preserved as cross-sections and originate in the silty sandstone unit (Fig. 3B). A few mollusk casts occur in them and are of the same species as those in the silty sandstone unit. The burrows extend down as much as 4 m into the cliff-forming sandstone unit and, except at the upper ends, are preserved as well-cemented sandstone casts that project from the more easily eroded sandstone matrix (Figs. 3C–E). It is these projecting spiral casts that inspired the locality and formational names (*tirabuzon*, Spanish for corkscrew). They occur wherever the upper part of the cliff-forming

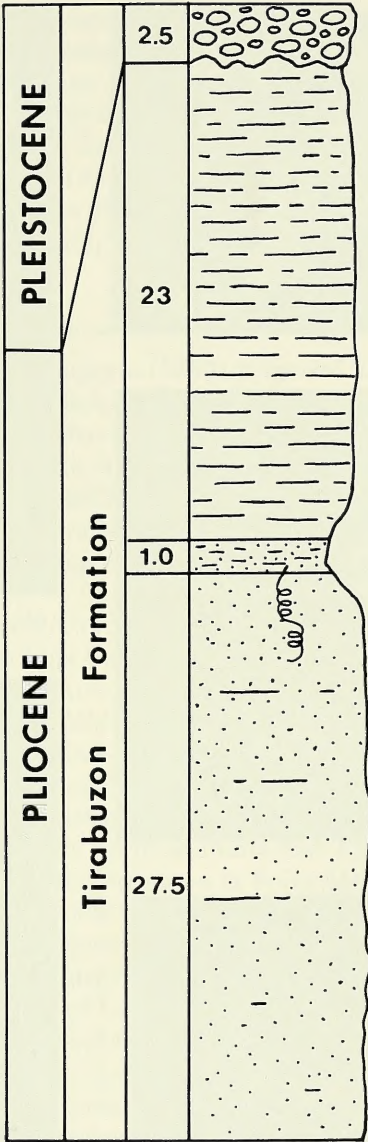
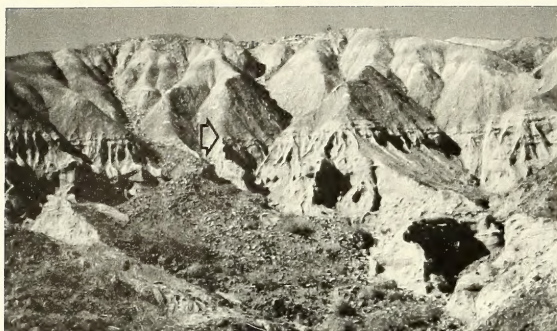


Fig. 2. Columnar section measured at southeastern end of Loma del Tirabuzon. Spiral symbol indicates stratigraphic position of *Gyrolithes*. Thicknesses in meters. See text for more complete description of units.

sandstone unit is exposed at Loma del Tirabuzon and at immediately adjacent areas northwest and southwest of the main cliff.

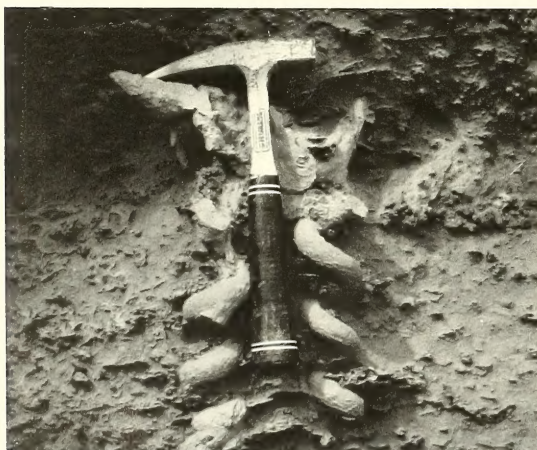
Loma del Tirabuzon recently has received more attention from paleontologists than any other exposure of the Tirabuzon Formation. DuShane (1977) described a new gastropod from there, Applegate (1978) and Applegate and Espinosa (1981) reported the shark fauna, Wilson (1981) noted the *Gyrolithes*, and Carreno (1982) studied the planktonic foraminiferan faunas. Despite some apparent contradic-



A



B



C



D



E

Fig. 3. Tirabuzon Formation *Gyrolithes* burrow systems at Loma del Tirabuzon. A, general view of section near southeastern end of Loma del Tirabuzon, approximate stratigraphic position of Fig. B at arrow. B, *Gyrolithes* burrow systems originating in silty sandstone (center) and extending downward into cliff-forming sandstone. C, adjacent sinistrally and dextrally coiled *Gyrolithes*. D-E, extensive *Gyrolithes* burrow systems.

tions in the published locality descriptions, these studies all are based on collections made at Loma del Tirabuzon.

The Tirabuzon Formation at Loma del Tirabuzon most recently has been reported to include both Lower and Upper Pliocene and possibly Lower Pleistocene strata (Applegate 1978; Carreno 1982). Previous determinations based on mollusks (Wilson and Rocha 1955) indicated the entire formation to be Middle Pliocene. These mollusks, some of which occur in the cliff-forming sandstone unit at Loma del Tirabuzon, probably indicate Upper Pliocene strata of more recent usage.

Previous Work on *Gyrolithes*

In the 100 years since de Saporta (1884) proposed *Gyrolithes* for spiral trace fossils from the Cretaceous of Belgium (type ichnospecies redescribed by Bromley and Frey 1974), similar fossils have been assigned to the genus from the Mesozoic and Cenozoic of Europe, North America, South America, and Asia (Hantzschel 1975, p. W65). Frey, Curran, and Pemberton (1984) broadly diagnosed the ichnogenus as "rarely branched, spiraled burrows; helix essentially vertical, consisting of dextral, sinistral, or reversing coils." The literature on *Gyrolithes* and related trace fossils is extensive.

In North America, *Gyrolithes* ranges from Cretaceous to Recent based on records in marine rocks from Baja California Sur, Mexico (Wilson 1981), California (Mansfield 1930; Boyer and Warme 1975; Cooley 1982), Coahuila, Mexico (Mansfield 1930), Maryland (Mansfield 1927), North Carolina (Powell 1977), Texas (Stenzel et al. 1957), and Virginia (Gernant 1972).

I have collected well-preserved *Gyrolithes* from two previously unrecorded west coast localities: 1), in the bed with the Late Oligocene marine mammal *Cornwallius* reported by Vanderhoof (1942) north of Punta San Telmo, Baja California Sur, Mexico, and 2), in the Trancas Formation at Point Mugu, Santa Monica Mountains, Ventura County, California, associated with the giant pectenid *Lyropecten nevadensis* (Conrad) and the gastropod *Turritella ocoyana* Conrad, indicating the Middle Miocene "Temblor" megafaunal stage. The specimens are deposited in the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (LACMIP locs. 6350 and 6920, respectively).

It is commonly agreed that *Gyrolithes* is organic in origin, but fossil spiral burrows have not yielded the remains of an animal that seems capable of having formed them. Powell (1977) reviewed published guesses about the nature of the animal and was first to assign to the genus Recent true spiral burrows. They were formed by the polychaete worm *Notomastus lobatus* Hartman, 1947 in the intertidal zone near Wrightsville Beach, North Carolina. Hertweck (1972, fig. 5a) previously had figured a similar Recent spiral burrow of *N. latericeus* Sars, 1850 from Georgia. Recent brachyuran crab burrows mentioned by Bromley and Frey (1974, p. 320) as being "spiral burrows corresponding to *Gyrolithes*" seem not to be true spirals comparable to *Gyrolithes* (Powell 1977, p. 553).

Description of the Loma del Tirabuzon Burrow Systems

The *Gyrolithes* at Loma del Tirabuzon are true spirals, oriented vertically and coiled sinistrally or dextrally (Figs. 3C, 4A, C-E, G-H). They have spiral axes 11 to 63 cm long with 5 to 11 whorls 5 to 9 cm in diameter. The burrow casts are



Fig. 4. Fragments of *Gyrolithes* burrow system casts from Loma del Tirabuzon. A, C–D, *Gyrolithes*. E, G–H, *Gyrolithes* and associated *Thalassinoides* “turnarounds.” B, F, I–K, *Thalassinoides* from *Gyrolithes* burrow systems, some with bifurcations and “turnarounds,” showing well-preserved “scratch marks” on B, J, and K. A–K are IGM hypotypes 3502–3512, respectively. All specimens $\times 0.33$. (Photos arranged for space efficiency and may not represent field orientations of specimens.)

2.5 to 4.5 cm in diameter (most are 3.5 to 4 cm), circular or slightly oval in cross section, with numerous, closely spaced, aligned, small ridges on all surfaces. These ridges represent depressions (scratches?) on the burrow walls (Figs. 4A, E, H). Many of the casts have shallow, longitudinal grooves 3 to 5 mm wide near the outside of the whorls (Fig. 4A) that may represent either preservational features or inhabitants with asymmetrical transverse outlines.

The *Gyrolithes* are integral parts of a complexly anastomosing burrow system that extends downwards from the silty sandstone into the cliff-forming sandstone for as much as 4 m and along strike for at least 0.6 km. Many of the burrows are so closely spaced that they nearly touch. The number of specimens is enormous.

The contiguous non-*Gyrolithes* parts of the burrow systems can be classified as *Thalassinoides* Ehrenberg, 1944. These casts have the same diameters as the *Gyrolithes*, with the same surface ornamentation (scratches? Figs. 4B, J-K), and, like them, are circular to oval in cross section. They may be vertical, horizontal, or inclined, straight or curved, with Y-shaped branches at irregular intervals and some thickened portions (turnarounds?) that are 5 to 7 cm in diameter and oval (dorso-ventrally flattened) in cross section (Figs. 4B, E, G-J). Distal ends of the burrows are represented by thickened "turnarounds" or gradually tapering pointed ends, both covered with scratch (?) marks.

Discussion

The Loma del Tirabuzon *Gyrolithes* is much larger both in whorl diameter (5 to 9 cm compared to 2.5 to 5 cm) and burrow diameter (2.5 to 4.5 cm compared to 1 to 2 cm) than any other *Gyrolithes* cited by Gernant (1972, table 1) in a summary of the dimensions of known *Gyrolithes*. The spiral burrows of the polychaete worms *Notomastus latericeus* and *N. lobatus*, referred to *Gyrolithes* by Powell (1977), are much smaller than the Loma del Tirabuzon *Gyrolithes*. In addition, the spiral axes of these worm burrows are variously oriented, some even horizontally (Hertweck 1972, fig. 5a; Powell 1977, p. 553), whereas the spiral axes of other *Gyrolithes*, including those at Loma del Tirabuzon, all are vertical. The abundant scratch (?) marks lining the burrows of the Loma del Tirabuzon *Gyrolithes* further distinguish it from specimens described from elsewhere, which are smooth or otherwise variously ornamented.

Fossils of animals capable of making the spiral burrows have not been found in the many *Gyrolithes* known from localities of various ages and areas of the world. A polychaete origin would explain their absence. On the other hand, the presence of apparent scratch marks on all parts of the Loma del Tirabuzon *Gyrolithes* system casts, especially the distal ends, suggests that these marks represent excavation and that the pointed distal ends were filled while being excavated. If this is true, then soft-bodied polychaetes are unlikely to have formed the burrow systems since they lacked hard parts capable of producing such marks. It seems more probable that decapod crustaceans made the burrows, as suggested by Hantzschel (1975, p. W65) and others. Why then have no fossil burrowing decapods been found associated with the burrows? Several workers in addition to me have searched without success for them at Loma del Tirabuzon.

If, as suggested by the field relations, the animals that formed the burrows at Loma del Tirabuzon were contemporaneous with the fossils in the silty sand layer,

then they lived in moderately deep waters of the neritic zone. Numerous specimens of the marine bivalve *Lucinoma annulata* (Reeve 1850) are represented in this unit by internal casts of paired valves in growth position. This species ranges from Late Miocene to Recent (Hertlein and Grant 1972, p. 247) and was reported by Keen (1971, p. 126) to be "... always an offshore species, dredging records being at depths of 55 to 90 m."

Powell (1977, p. 554) thought that previously reported associations of *Gyrolithes* and *Thalassinoides* could be accounted for by pirating or accidental intrusions into one kind of burrow by the animal of the other. I do not believe this to be the case with the Loma del Tirabuzon burrow systems because, 1) both the *Gyrolithes* and *Thalassinoides* universally have scratch marks on their walls formed by one kind of animal but not a polychaete; 2) the entire burrow system is composed of morphologically similar *Gyrolithes* and *Thalassinoides* that repeatedly merge; 3) the *Gyrolithes* are formed at various levels within the upper part of the cliff-forming sandstone but have no communication with the surface of the formation other than through *Thalassinoides*. It could be that a polychaete entered existing *Thalassinoides*, descended to various depths and there formed *Gyrolithes*, which were later incorporated by the *Thalassinoides* animals for their burrow systems. However, there are no smooth-tunnel *Gyrolithes* at Loma del Tirabuzon of the polychaete type. In addition, this hypothesis seems unnecessarily complex in view of the simple fact that the burrow system at Loma del Tirabuzon appears visually to be a single system.

The different kinds of burrow morphologies currently assigned to *Gyrolithes* suggest that it is a polyphyletic ichnogenus in need of revision. Perhaps *Xenohelix* Mansfield, 1927 (type ichnospecies *X. marylandica* Mansfield, 1927 from the Miocene of Maryland) should be reinstated for the generally tightly coiled burrows of Cenozoic age and *Gyrolithes* should be restricted to the more openly coiled burrows typical of the type ichnospecies from the European Cretaceous. Neither of these names is suitable for the spiral burrows with randomly oriented axes made by polychaete worms.

Documentation

The stratigraphic interval containing the *Gyrolithes* burrow systems at Loma del Tirabuzon as described above has been assigned Natural History Museum of Los Angeles County, Invertebrate Paleontology Section locality number 4828. The hypotypes shown on Fig. 4 are from this locality and have been assigned specimen numbers of the Museo de Paleontología de Invertebrados, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, México, D.F. (abbreviated IGM).

Acknowledgments

I am indebted to Shelton P. Applegate for introducing me to Loma del Tirabuzon and its *Gyrolithes*, to Ismael Ferrusquia and Diego A. Cordoba for providing permission to pursue field work in Mexico, to Eric N. Powell for writing me about *Gyrolithes*, to Phillip Owen for assistance in the field, and to the Natural History Museum of Los Angeles County and its Foundation for support.

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Accepted for publication 20 May 1984.

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Bryozoa from Seagrass Beds of the Northern Saudi Arabian Coast: Distribution and Seasonality

John D. Soule and Dorothy F. Soule

Abstract.—Bryozoa from seagrass beds of the Northern Saudi Arabian coast by John D. Soule and Dorothy F. Soule. *Bull. Southern California Acad. Sci.*, 84(2): 67–75, 1985. Four subtidal surveys of seagrass and sandbeds at eight stations on the northern coast of Saudi Arabia yielded 29 species of bryozoans in 1.0 mm and 0.5 mm screenings of 0.1 m² replicates. The most common species was the cyclostome *Lichenopora radiata* (21%). Species composition was 15% cosmopolitan (except Arctic); 14% circumtropical-subtropical and 61% Indo-Pacific. Temperatures ranged from 16.9° to 34.4°C and salinities ranged from 40 to 50‰ during collecting.

Seagrass beds constitute valuable inshore biological resources as habitats and substrata for many invertebrates and fishes; coastal development can endanger such habitats, and measures to protect them from impact are needed. Four subtidal survey of seagrass beds along the northern coast of Saudi Arabia, in connection with petroleum development plans by ARAMCO, were conducted in 1981–1982. Bryozoans sent to the authors for identification provide the first records of that fauna from the Saudi Arabian (Persian) Gulf (Figs. 1, 2). Extensive records exist for the southern Mediterranean Sea (e.g., Savigny 1817?; Audouin 1826; Gautier 1961; Powell 1969a), and the Red Sea (e.g., Waters 1909, 1910; Harmer 1926, 1957; Hastings 1927; Powell 1967, 1969b; Redier 1971; Dumont 1981). Fewer records exist for the Arabian Sea off the coast of Pakistan and India (e.g., Menon and Nair 1971; Menon 1972; Menon et al. 1977), while the Persian Gulf has apparently not previously been sampled.

Methods

Subtidal collecting methods were designed primarily to obtain infaunal and epifaunal organisms other than bryozoans such as crustaceans and polychaetes, and hence the techniques were not optimal for obtaining bryozoans. Thus bryozoans were probably very much under-represented in the collections for the general area. Samples were collected in four quarters; September 1981, November 1981, February–March 1982, and April–May 1982. For each period, 48 samples were collected, consisting of three replicates each of two biotopes, sand and seagrass, at eight stations. The 0.1 m² replicates were washed through 1.0 and 0.5 mm sieves and the residues stained with bengal red. Samples were frozen due to prohibitions on alcohol in Saudi Arabia and difficulties with permits for the use of formalin. Samples were reconstituted in isopropyl alcohol in the USA before distribution to systematics specialists. Calcareous specimens were air dried and mounted on slides for identification.

Results

A total of 29 species were identified in the screened material of which 11 were cheilostome anascans, 14 were cheilostome ascorophorans, two were cyclostome



Fig. 1. Study site (box) on northern Saudi Arabian coast of Persian Gulf.

species and two were ctenostomes. The ranking of stations according to numbers of occurrences of colonies, regardless of species, showed that three areas had relatively high counts (Fig. 2); station 3 was first with 77 occurrences, station 1 was second with 72, and station 5 was third with 68. A second cluster of stations were grouped as stations 2, 6, and 4, with counts totalling 51, 42, and 40 respectively, followed by a grouping with lower numbers, stations 7 and 8, which had 27 and 21 occurrences respectively. The stations are listed in Table 1, with short descriptions. The grouping of station 1 with stations 3 and 5 is somewhat surprising, since station 1 is on the open coast whereas stations 3 and 5 are in embayments. The species are listed in Table 2, with the occurrences at each station according to the two biotopes, sand and seagrass. A total of 398 occurrences was recorded.

Species Distribution

The species with the most occurrences, 85, was *Lichenopora radiata* (Audouin 1826), which greatly exceeded all others (Table 2). It was most prominent at stations 2 and 3. *Lichenopora* spp. are known to encrust seagrass blades; *L. radiata* was originally illustrated as being on *Fucus*, while *L. buskiana* and *L. novaezealandiae* were found in Scammons Lagoon, Baja California encrusting on eelgrass and forming windrows of dead colonies along the high tide line (Soule and Soule 1964a).

Antropora marginella (Hincks 1884) was the second most numerous species, having 58 occurrences, with 11 each at stations 3 and 5. It was originally described

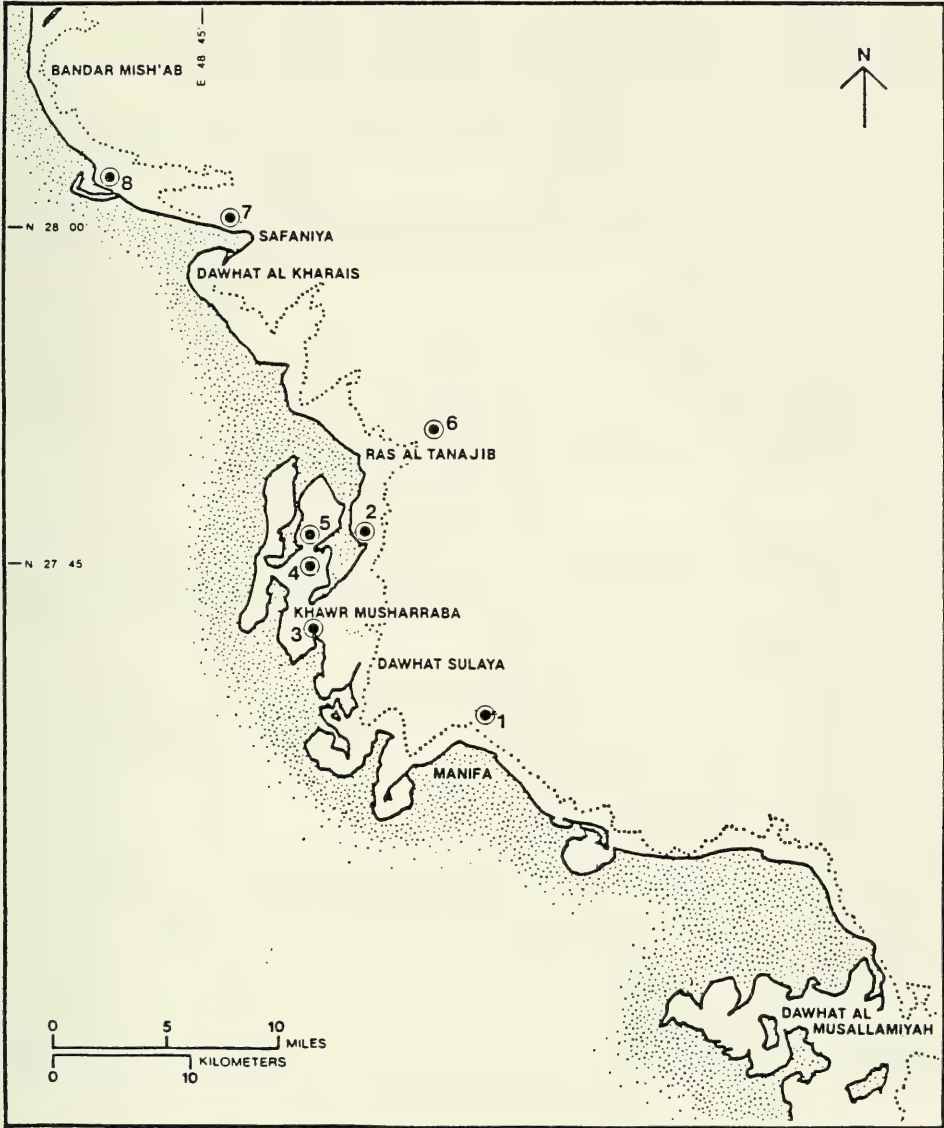


Fig. 2. Sampling stations in the vicinity of the Northern Area Development Project.

from the Indian Ocean coast of Burma but has been reported from other limited Indo-Pacific localities such as Ceylon, the Malay peninsula, and New Guinea.

Thalamoporella gothica (Busk 1856) had 54 occurrences, with 16 at station 3, 11 at station 5, and 9 at station 2. This species was originally described from Mazatlan, Mexico opposite the tip of Baja California (Soule 1959). The species apparently has a disjunct distribution, occurring in the Indian Ocean but it was not found in the mid-Pacific Islands (Soule and Soule 1964b, 1970). Although old records indicate that variations of this species were found in the Indo-Pacific, it is not possible to determine with certainty what the species were because no

Table 1. Station descriptions.

Station 1.	Near coral reef off Manifa GOSP; depth of sand and grass samples 10 ft (3 m).
Station 2.	Near proposed site of Ras Tanajib marine facility, south of small coral reef offshore of well; depth of sand and grass samples 8 ft (2.4 m).
Station 3.	Middle of Manifa Bay entrance channel; depth of sand and grass samples 4 ft (1.3 m).
Station 4.	Middle of Manifa Bay; depth of grass and sand samples 4 ft (1.3 m), some sand dollars in sand area.
Station 5.	Northeastern Manifa Bay about 1000 m inside from mouth; depth of grass samples 4 ft (1.3 m); sand 6 ft (1.3 m); grass station with many pen shells; sand with many sand dollars in patches.
Station 6.	Off shore from Ras Tanajib about 2 mi, near buoys between channel marker beacons 8 and 9; depth of grass samples 6 ft (1.8 m), sand 4 ft (1.3 m). Many <i>Pinna</i> and <i>Pinctada radiata</i> in grass area.
Station 7.	Between Safaniya Pier and jetty offshore from Safanuja flares, northwest of row of pipeline signs; depth of grass and sand samples 8 ft (2.4 m).
Station 8.	Off Bandar al Mishab between rock pile and Mishab in small embayment north of Bundar al Mishab rocks; depth of grass samples 8 ft (2.4 m), sand 3 ft (2.4 m).

determinations were made of the internal calcareous spicules, the shapes of which are species-specific. It may well be that Hinck's variety *indica* is actually a separate Indo-Pacific species and is not identical to *T. gothica*, but the fragments collected were too small for further analysis.

Parasmittinid species were well represented, with three of the species *P. egyptiaca*, *P. unispinosa*, and *P. dentigera*, having substantial numbers at stations 3, 5, and 6. The species are all known from the Red Sea, Indian Ocean, and Malaysian-New Guinea region but have not appeared in Pacific island collections to date (Soule 1973).

Two other species occurred in substantial numbers, *Celleporaria labelligera* Harmer 1957, and *Watersipora subtorquata* (d'Orbigny 1852). The former is known from the Red Sea and a few Malay sites and was prominent at stations 2 and 3. The latter is a common tropical and subtropical fouling species. Since the type locality for *W. subovoidea* (Audouin 1826) is probably in the Red Sea, that name would be expected to take precedence. However, there is no type or description and the Savigny illustration does not distinguish it from more or less similar forms (Soule and Soule 1975, 1983) found in the Mediterranean, Indo-Pacific, and Caribbean-Atlantic. Since the material found is similar to the type specimen of *W. subtorquata*, photographed by us, we continue to use that name until a lectotype is designated for *W. subovoidea*. The occurrence of this fouling species at stations 1 and 7 may result from the extensive shipping activity along the Gulf.

Of the remaining species, 15 species showed only one to three occurrences and five species had four to seven occurrences.

Species Composition

Fifteen percent of the species reported appear to be virtually cosmopolitan in distribution and thermal tolerance. These include *Bugula neritina*, *Bugula stolonifera*, *Membranipora tuberculata*, *Membranipora membranacea*, *Schizoporella unicornis*, *Bowerbankia gracilis*, and *Aeoverrillia setigera*. These species (*sensu lato*) occur virtually world-wide in tropical and temperate waters as fouling organisms.

Table 2. Bryozoan species occurrences at eight stations in seagrass bed biotopes.

No. of occurrences in sand (S) or grass (G)	Station																Total
	1		2		3		4		5		6		7		8		
	S	G	S	G	S	G	S	G	S	G	S	G	S	G	S	G	
Species																	
<i>Thalamoporella gothica</i> (Busk 1856)	2	5	4	5	5	11	2	3	2	9	1	1	1	1	0	2	54
<i>Antropora marginella</i> (Hincks 1884)	6	1	1	8	5	6	2	2	3	8	2	7	1	1	1	4	58
<i>Bugula neritina</i> (Linnaeus 1758)																	2
<i>Bugula stolonifera</i> Ryland, 1960	1						1										1
<i>Caulibugula zanzibariensis</i> (Waters 1913)		2															2
<i>Membranipora tuberculata</i> (Bosc 1802)		1	1	1	1	1				1					1	1	7
<i>Membranipora membranacea</i> (Linnaeus 1767)																	1
<i>Scrupocellaria spatulata</i> (d'Orbigny 1851)								1									1
<i>Synnotum aegyptiacum</i> (Audouin 1826)	1							4		2							7
<i>Savignyella lafonti</i> (Audouin 1826)	1							1									2
<i>Nellia quadrilatera</i> (d'Orbigny 1851)								1		1							2
<i>Parasmittina signata</i> (Waters 1889)																	2
<i>Parasmittina raigii</i> (Audouin 1826)	1													1			1
<i>Parasmittina egyptiaca</i> (Waters 1909)	4	2	1	1	1		1			2	6	5	1				24
<i>Parasmittina unispinosa</i> (Waters 1889)	1			2	2	6	1	1	1	4	2	3					23
<i>Parasmittina denigera</i> (Harmer 1957)	1		1		4	5	1	4	4	9	3	2					34
<i>Rhynchozoon larreyi</i> (Audouin 1826)	4	1			2	3			1	3							14
<i>Hippodiplosia ottomulleriana</i> (Moll 1803)	1									3						1	5
<i>Tremogasterina robusta</i> (Hincks 1884)	3																3
<i>Schizoporella unicornis</i> (Johnston 1847)	1	1												1			3
<i>Schizoporella errata</i> (Waters 1878)													1				1
<i>Celleporaria labelligera</i> Harmer, 1957	3	1	3	3	2	5	1				1	1	3	1	1	1	26
<i>Microporella orientalis</i> Harmer, 1957	3									1							4
<i>Arthropoma cecili</i> (Audouin 1826)	3																3
<i>Watersipora subtorquata</i> (d'Orbigny 1852)	2	8		1	2		1	1	1	1	1	1	4	3	1		26
<i>Lichenopora radiata</i> (Audouin 1826)	1	7	4	14	2	14	2	8	2	9	2	5	2	5	1	7	85
<i>Crista elongata</i> Milne Edwards, 1838																	6
<i>Aeverillia setigera</i> (Hincks), 1887	4							1		1							1
<i>Bowerbankia gracilis</i> Leidy, 1855																	1
Totals	36	36	15	36	25	52	12	28	14	54	18	24	14	13	5	16	398

Table 3. Sea temperature and salinity during sampling program.

Sta- tion	8-13 September 1981			18-23 November 1981			28 Feb.-9 March 1982			20 April-1 May 1982		
	Temp.		Sal. ‰	Temp.		Sal. ‰	Temp.		Sal. ‰	Temp.		Sal. ‰
	C	F		C	F		C	F		C	F	
1	32.2	90	40	21.1	70	45	16.9	62.5	42	24.5	76	42
2	34.4	94	40	22.2	72	42	18.4	65	41	26.7	80	44
3	32.8	91	43	21.1	70	48	17.2	63	42	27.2	81	42
4	32.8	91	42	20.6	69	49	18.4	65	44	26.7	80	42
5	34.4	94	43	20.0	68	50	18.4	65	42	26.1	79	43
6	32.2	90	40	22.2	72	42	17.8	64	41	25.6	78	42
7	32.8	91	42	17.8	64	44	17.8	64	41	25.0	77	41
8	33.3	92	42	17.2	63	41	17.8	64	41	25.6	78	40

They may, however, be quite transient as suggested by their low numbers, and they did not appear in the hottest part of the year sampled (September).

Another 14% appear to be circumtropical and subtropical species, also prominent in fouling communities. These include *Synnotum aegyptiacum*, *Savignyella lafonti*, *Watersipora subtorquata*, and *Crisia elongata*. However, their numbers of occurrences equalled only 14% of the total collection, and if the common *Watersipora subtorquata* is excluded the others constitute only 8%.

The remaining 61% of the collection is composed of species which are generally limited to the Red Sea, the Indian Ocean, and the seas between Australia, Indonesia, Malaysia, and New Guinea; the Indo-Pacific center of distribution. They have not, to date, been reported in the mid-Pacific Islands or the eastern Pacific.

Temperature and Salinity Tolerance

The Persian Gulf is subject to extremes in water temperature and the stations along the Saudi Arabian northern coast showed high salinities as well (Table 3). The lowest water temperature recorded during the present collecting was 16.9°C (62.5°F) on 28 February 1982 at station 1, with temperatures ranging up to 18.4°C (65°F) during the study. The Persian Gulf area falls between the 10° and 16°C isotherms for normal January temperature (Espenshade 1982) which is within the warm-temperate winter range of 10° to 20°C. However, the normal July temperature (op. cit.) lies between the 27°C tropical isotherms. No July collections were made in present study, but September water temperatures ranged from 32.2°C (90°F) to 34.4°C (94°F) during collecting, well above the 25°C defined as the maximum for tropical summer temperatures.

Salinities were high at the stations sampled, ranging from 40 to 50‰. These figures were unexpected for species usually found in oceanic salinities in the 33 to 37‰ range. The highest salinities found occurred during November collecting. Euryhaline organisms are generally associated with the hyposalinity of estuarine environments or coastal areas affected by rainfall and runoff. Reports of hypersaline organisms are limited primarily to crustaceans such as *Artemia*, the brine shrimp; however salinity tolerances of bryozoans extend to 38-40‰ in the Red Sea (Marcus 1926), and may well be higher in that similarly arid region subjected to high rates of evaporation.

In grouping the species occurrences on the basis of season (Table 4), the hottest

Table 4. Seasonality of bryozoan species.

	Sept 81	Nov 81	Feb-Mar 82	Apr-May 82	Totals
<i>Thalamoporella gothica</i>	7	12	22	13	54
<i>Antropora marginella</i>	4	19	19	16	58
<i>Bugula neritina</i>		1	1		2
<i>Bugula stolonifera</i>			1		1
<i>Caulibugula zanzibariensis</i>		1	1		2
<i>Membranipora tuberculata</i>	1	1	2	3	7
<i>Membranipora membranacea</i>				1	1
<i>Scrupocellaria spatulata</i>			1		1
<i>Synnotum aegyptiacum</i>		3	4		7
<i>Savignyella lafonti</i>			2		2
<i>Nellia quadrilatera</i>		1	1		2
<i>Parasmittina signata</i>		1			1
<i>Parasmittina raigii</i>			1		1
<i>Parasmittina egytiaca</i>	4	6	7	7	24
<i>Parasmittina unispinosa</i>	3	9	7	4	23
<i>Parasmittina dentigera</i>	4	9	13	8	34
<i>Rhynchozoon larreyi</i>	1	4	8	1	14
<i>Hippodiplosia ottomulleriana</i>	1	1	2	1	5
<i>Tremogasterina robusta</i>		1	1	1	3
<i>Schizoporella unicornis</i>			2	1	3
<i>Schizoporella errata</i>			1		1
<i>Celleporaria labelligera</i>	4	11	5	6	26
<i>Microporella orientalis</i>		2	1	1	4
<i>Arthropoma cecili</i>		2	1		3
<i>Watersipora subtorquata</i>	3	8	10	5	26
<i>Lichenopora radiata</i>	12	21	21	31	85
<i>Crisia elongata</i>	1		3	2	6
<i>Aeverrillia setigera</i>		1			1
<i>Bowerkbankia gracilis</i>			1		1
Totals	45	114	138	101	398

tropical September period showed only 12 species present, with total numbers less than half the next highest period. All of the species present in September occurred in all seasons sampled except for *Crisia elongata*, which was absent in November. Its numbers were so low that this could be entirely due to the sampling error. For the most part the temperature-tolerant species were also those with the most numerous occurrences, but even those showed much reduced numbers in September.

The peak period was February-March 1982 with 138 occurrences; second was November 1981, with 144 occurrences, and April-May with 101 occurrences.

Conclusion

The eight stations sampled represent only a small area of the Saudi Arabian northern coast, where oil development is underway. However, collections made from the seagrass beds represent the first records for the Persian Gulf as far as we can determine. The bryozoan fauna was rich for such limited substrata, and in consideration of the restrictive techniques used to collect and sort. Additional collecting at the same stations is expected, but unfortunately no collecting has been done at the local coral reefs, which probably would host many more species.

Acknowledgments

These investigations were funded by ARAMCO, through contracts with Saudi Arabian Tetra-Tech, Ltd. Appreciation is expressed in particular to Dr. John McCain, the director of environmental programs who supervised the collecting, shipping, and reporting, and to Dr. Robert Pastorok. Dr. McCain is presently at the Saudi Arabian University of Petroleum and Minerals.

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Accepted for publication 20 May 1984.

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Domestic Dog Associated with Human Remains at Rancho La Brea

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Abstract.—Domestic dog associated with human remains at Rancho La Brea by Richard L. Reynolds. *Bull. Southern California Acad. Sci.*, 84(2):76-85, 1985. In 1914, human remains were discovered in an asphalt deposit at Rancho La Brea, California. The skull and mandible of a small domestic dog (*Canis familiaris*) together with a number of shell and stone artifacts were found associated with the human skeleton and all appear to date at 9000 ± 80 years before present. Re-examination of all available data indicates this occurrence is a secondary burial (reburial) rather than a primary interment, accidental entrapment, or the concealment of a homicide victim, as previously suggested.

In the early part of this century (1914), during scientific excavations at the late Pleistocene-Holocene Rancho La Brea asphalt deposits, a notable discovery was made. Human remains were encountered in Pit 10 of the Los Angeles County Museum of Natural History (LACM) excavations (Merriam 1914; Wyman 1915; Hrdlička 1918). These remains, the so-called La Brea Woman, represent a female aborigine about 25 years of age and of probable Chumash racial affinities (Kroeber *vide* Merriam 1914; Kroeber *vide* Hrdlička 1918; Kroeber 1962). On the basis of cranial morphology, this individual is referable to the *Narrow-Nosed* subtype of the *Californian* physical type of Gifford (1926).

Most of the mammalian fauna associated with the human was sent to the University of California, Berkeley, for study in 1914. The unexamined collection remained there in wooden crates until 1945 when it was returned to the LACM. The author, while curating these materials in 1967, discovered the fragmentary skull and mandible of a small domestic dog, *Canis familiaris* (Reynolds 1979a) along with a number of shell and stone artifacts. This report concerns mainly the domestic dog and evidence supportive of reburial. Detailed studies of the Pit 10 fauna, La Brea Woman, and artifacts from Rancho La Brea are currently in progress (Reynolds et al. mss in prep.).

Material

The skull and mandible (Fig. 1) of specimen number LACMHC (Hancock Collection) 6260, is that of a small adult dog (basioccipital-basisphenoid suture closed) with teeth in moderate wear. The overall length of the reconstructed skull is 144.0 mm (measurements in Table 1). Portions of the right side of the cranium and both zygomatic arches are missing. As is typical of most domestic dog varieties, the frontal sinuses are inflated giving the forehead a steepness not found in wolves and coyotes. Orbital angle (after Iljin 1941; Mech 1970) is approximately 55 degrees. The sagittal crest shows no development except in the interparietal region. Maxillary root of the zygomatic arch is weakly buttressed. The damaged tympanic bullae show some reduction but are not rugose or flattened. There are no P1/ alveoli. The left P2/, P4/, and the anterior half of the right P4/ are the

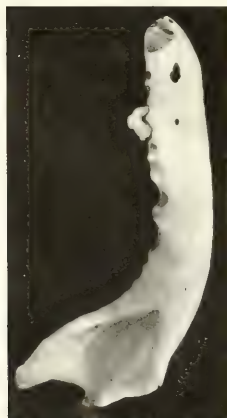
Table 1. Measurements of LACM HC 6260 in millimeters (mm). * = Estimate, L = Length, W = Width, H = Height, Ant. = Anterior, Post. = Posterior.

Character	Left	Axial	Right
Skull L		144.0	
Condylbasal L		135.3	
Skull Base L		128.8	
Bizygomatic W		85.2*	
Interorbital W		29.8*	
Least W. Rostrum		25.9	
Greatest W. Palate		53.8	
Postorbital Constriction		29.6*	
W Postorbital Processes		36.6*	
Facial L		68.0	
Cranial L		82.2	
Cranial W		49.6*	
Upper Tooth Row L	72.1		72.1
P4/ Crown L	15.7		
P4/ Crown W	8.2		
Alveolar L Post. C/ to Post. M2/		49.7	
Mandible L	103.0		103.0
Mandible W below M/1	7.8		8.0
P/3 Crown L	8.2		8.8
P/3 Crown W	4.0		4.1
P/4 Crown L	10.0		
P/4 Crown W	4.8		
M/1 Crown L	18.2		
M/1 Crown W	6.8		
M/2 Crown L	7.5		
M/2 Crown W	5.6		
Lower Tooth Row L	71.0		72.6
W Ant. Base Ascending Ramus	6.0		6.9
H Ascending Ramus Parallel to Post. Margin	37.7*		37.7
Minimum W Symphysis Post. to /C	8.2		8.2
Alveolar L Post. I/1 to Post. P/2	19.7*		21.0*

only teeth present in the upper dentition. The misshapen left P2/ is unerupted and impacted deep in the alveolar margin. Secondary resorption of the left DP2/ alveolus is possible due to an abscess evident laterally on the maxilla. Due to the abrupt narrowing of the rostrum, the P3/ alveoli are oriented at about a 55 degree angle with respect to the long axes of the P4/'s. A transverse line at the end of the palate falls through the middle of the M2/ alveoli.

Both right and left rami of the mandible are present. The inferior margin of the mandible is convex in profile with no marked slimming in the premolar region. The left coronoid, both condyloid, and angular processes are incomplete. The apex of the right coronoid process is intact and is directed posteriorly. A "turned-back" apex of the coronoid process is generally a good diagnostic character in domestic dogs (Olsen and Olsen 1977). Left mandibular teeth present are P/3-M/2, with only the P/3 present on the right. There are no P/1 alveoli. The lower teeth are closely spaced but not crowded, with the P/2-P/3 diastema 1.0 mm in length. The hypoconid on the talonid of the M/1 is more than twice the size of the entoconid.

All external surfaces of the skull and mandible exhibit "pit wear" due to abrasion

**B****A****C****D**

caused by sand grains suspended in the asphaltic matrix. It is thought that escaping methane gas and possibly other forces, such as earth tremors, over long periods of time create slight movements which result in a sandpapering or grooving effect on bones from Rancho La Brea (Merriam 1914; Hrdlička 1918; Stock 1929; Miller 1969; Berger, Protsch, Reynolds, Rozaire, and Sackett 1971). Because of this phenomenon and the fragmentary nature of the specimen, some of the measurements given in Table 1 are estimates.

The Deposit

The asphalt deposits are located on the Santa Monica Plain 4.0 km south of the Santa Monica Mountains and 13.7 km northeast of the Pacific coast (Latitude 34°3'49"N, Longitude 118°21'22"W, 7.5' topographic map, United States Geological Survey, Hollywood, California, 1966 edition). Here, late Pleistocene alluvial sediments consist of clays, sands, gravels, and cobbles derived from the southern slopes of the Santa Monica Mountains. These overlie petroleum-bearing marine beds of Tertiary age. In the vicinity of Rancho La Brea, localized structures in the older strata allow trapped petroleum and natural gas to seep upward through the Pleistocene sediments to the surface.

The escape of petroleum over long periods of time occasionally created enlarged vents. The excavation of Pit 10 revealed the presence of two such vents, a north and a south vent, filled with dark asphalt. Each vent measured about 0.9 m in diameter and contributed to a hard asphaltic layer at the surface. At a depth of about 2.4 m below datum the vents opened into a single large dome-shaped asphalt mass of not less than 2.4 m in diameter, extending downward to an unknown depth. Both vents joined the large asphaltic mass on the northeast side. The south vent was roughly vertical while the north vent extended approximately 1.8 m horizontally to the northeast before abruptly sloping to the surface. The domestic dog, the human remains, and the shell and stone artifacts occurred in the north vent. The dog material was found between 1.2 and 1.7 m, the human bones were distributed between 2.0 and 2.7 m, and the artifacts ranged between 2.0 and 4.0 m.

The north vent penetrated a small late Pleistocene bone-bearing asphalt pocket near the surface. The older asphalt occurred as oxidized lumps in the dark matrix between 1.2 and 1.7 m and contained isolated elements of at least three extinct mammals: the Sabre-tooth Cat, *Smilodon californicus*; the American Lion, *Felis atrox*; and the Western Horse, *Equus occidentalis*. An extinct avifauna was also present (Howard and Miller 1939). Specimens of extinct mammals in the north vent are either friable and light in color, or show no evidence of pit wear. In contrast, non-extinct mammals, including the dog and human material, are well preserved, dark in color, and show considerable pit wear.

Radiocarbon dates using the bone collagen method (Ho, Marcus, and Berger 1969) confirms a late Pleistocene age for the extinct mammals in the north vent, an early Holocene age for the non-extinct mammals in the north vent, and a sub-

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Fig. 1. *Canis familiaris* LACM HC 6260. Skull in left lateral view (A), ventral view (B), and mandible in labial views of left ramus (C) and right ramus (D). All stereographic pairs coated with ammonium chloride and photographed with a Baird Stereo-Bar. $\times 0.5$.

Recent age for the south vent. A left femur (LACMHC 6945) of a juvenile extinct horse (*Equus occidentalis*) from the north vent was dated at the University of California, Los Angeles (sample number UCLA-1292CC) and was found to be $15,700 \pm 530$ BP (Before Present). Dating of the human remains (UCLA-1292BB), using a left femur (LACMHC 1323), at 9000 ± 80 BP (Berger et al. 1971) indicates that they are early Recent (Holocene) in age. By association, the age of the domestic dog and the artifacts is also about 9000 BP. The south vent, which contained no extinct mammals, was found to be of more recent origin. The left femur (LACMHC 133) of a young female grizzly bear (*Ursus arctos*) from a depth of 1.2 m in the south vent was radiocarbon dated by Queens College, New York (QC-916R) at 5270 ± 155 BP.

Aboriginal Dogs

There were three varieties of aboriginal domestic dogs in the southwestern United States: a small short-nosed form (Pachycyon); a small slender-nosed form (Techichi); and a larger generalized form (Plains-Indian dog) (Allen 1920). These varieties of dogs were not true breeds but merely mongrel morphotypes and though variations occur, most Indian dogs of the prehistoric American southwest fit one of these three mongrel varieties. Measurements and cranial morphology of the dog from Pit 10 fit Allen's (1920) description of the Techichi. Its most distinctive features are small size and delicate rostrum, giving it a fox-like appearance.

Techichi remains have been identified from sites in the southwestern United States, the Yucatan area of Mexico, and northwestern South America (Allen 1920). This variety of dog was encountered by early explorers and others who reported seeing small dogs of fox-like appearance. They were light-limbed, of rather slender proportions, with narrow delicate heads, fine muzzles, erect ears, and well developed tails, which may have been close-haired. Colors were reported as black, black and white, and brownish. The widespread temporal and geographic range of the Techichi testifies to its popularity as a companion or food item of pre-Columbian Indians.

The presence of this aboriginal dog near the remains of La Brea Woman is considered significant. Driver (1969) lists domestic dogs among animals sacrificed by most New World Indians at the death of their owners to propitiate the supernatural. Domestic dog burials of pre-Columbian age are relatively rare in the United States, and most are reported in the southwest (Allen 1920; Lawrence 1944; Olsen 1968, 1972). Allen (1920) reports the Greenland Eskimo custom of placing the head of a dog in a human burial to guide the deceased to the Land of Souls because "a dog can find its way everywhere," and a similar custom among the Yucatan Mayas, the dog to carry its master's soul across the "Chicunauhapan" or nine-fold flowing stream. Burial of dogs with humans, probably for similar supernatural reasons, is documented in California (Bean and Smith 1978; Elsasser 1978b; Lapena 1978). Bean and Smith (1978) report the island Gabrielino custom of burying a dog over the body, and there is some indication this was also an island Chumash practice (Phil C. Orr, pers. comm. 1971).

Discussion

The unusual occurrence of associated artifacts and human and dog remains in an asphalt deposit at Rancho La Brea can now be re-evaluated. Explanations

offered to account for the human remains in Pit 10 include: accidental entrapment (Hrdlička 1918; Heizer 1943); execution (George C. Page Museum exhibit label copy 1977); homicide and/or disposal of a body in asphalt in a non-burial context (Hrdlička 1918; Cyril B. Courville, pers. comm. 1967; Reynolds 1968; Berger et al. 1971; Bromage and Shermis 1981); burial (Hrdlička 1918); and reburial (this report).

Although it is impossible to determine the ground surface conditions of 9000 years ago, accidental entrapment of a healthy adult human is quite unlikely. Since 1914, the Pit 10 excavation has filled to surface level with a pool of asphalt approximately 4.8 m in diameter. Experience has shown that on the hottest days in summer only the top several centimeters becomes viscous. A human stepping on this surface sinks so slowly that it can easily escape. In winter and on cool spring and fall days the surface of Pit 10 is solid enough to walk upon.

It was thought that La Brea Woman suffered from a severe sinus infection and "Tribe members, suspecting she was possessed may have disposed of her in the pits, hoping that her evil spirits would be trapped by the asphalt" (George C. Page Museum exhibit label copy 1977). This interesting notion was based on two misconceptions. Normal frontal sinuses exposed by pit wear were interpreted as a diseased condition. An x-ray diagnosis was made by a pathologist inexperienced with archaeological crania. Asphaltic matrix inside the skull was mistaken for diseased bone tissue.

The theory that La Brea Woman was a victim of homicide and her body was disposed of (or "thrown") in the north vent of Pit 10 is based on the fragmented condition of the reconstructed cranium. The cranium was badly abraded and broken when found. Upon gross examination, some of the fractures resemble traumatic lesions caused by impacts from a heavy blunt instrument (Cyril B. Courville, pers. comm. 1967; Reynolds 1968; Berger et al. 1971; Bromage and Shermis 1981). Bromage and Shermis (1981) concluded that, "This particular skeleton, dated at over 9000 years BP, gains it[s] importance as one of the oldest homicides, if not the oldest homicide, in the New World. It is likely that she was murdered, evidenced by the fracturing of the cranium, and then her body thrown into the Tar Pits, perhaps to conceal the deed."

The only previous mention of burial among other possibilities to account for the human presence in Pit 10 was by Hrdlička (1918): "There is a possibility that the bones may have found their way into the asphalt from a grave, but a body may also have sunk in the pit accidentally or have been introduced."

The presence of the human remains, Techichi, and artifacts in Pit 10 is consistent with secondary interment or reburial. Reburial was a common and widespread practice by southern California Indians (Kroeber 1925; Walker 1951; King 1969; Grant 1978; Wallace 1978a; Gutman 1981). The incompleteness and fragmentary nature of the skeleton of La Brea Woman indicates reburial rather than primary interment. Skeletal elements recovered include skull, mandible, two cervical vertebrae, two lumbar vertebrae, one rib, left innominate, left scapula, distal portion of the right humerus, and the proximal portions of right and left ulnae, left radius, and right and left femora. When gathering up the remains from a temporary grave into a reburial bundle, no apparent attempt was made to locate all the bones. Usually, only the larger elements including the head, major long bones, pelvis, scapulae, a few ribs, and a few vertebrae were collected. Isolated

human teeth, vertebral and rib fragments, and small bones (particularly of the hands and feet) are common in southern California seasonal sites lacking cemeteries and probably result from this practice (Reynolds 1979b; Gutman 1981). Reburial may have its origin in some desire of the deceased to be interred near relatives (J. P. Harrington *vide* King 1969) or in the place of birth (Wilson and Towne 1978), and was probably associated with the Annual Mourning Ceremony (Walker 1951). Individuals who died during the yearly round of seasonal movements were placed in temporary graves and retrieved later for reburial in a mortuary village.

Associated with the partial human skeleton, in addition to the Techichi skull and mandible, were six fragments of marine mollusc shell (two of which were rectangular imperforate *Laevicardium* ornaments and four were highly polished *Tivela* fragments), and a skillfully "killed" (ceremonially defaced) mano. Personal property of the deceased was "killed" (releasing its spirit) to render it useless to grave robbers, to sever all familiar ties between this world and the deceased's ghost, and to aid the deceased in the next world. Such objects are typical of grave offerings in California (Kroeber 1925; Beardsley 1971; Bright 1978; Elsasser 1978a; Grant 1978; Wallace 1978b, c). Very little is known about southern California mortuary practices prior to about 8000 BP. In the following period, from 8000 to 5000 BP, disposal of the dead followed more than one practice in some communities. Flexed burials, extended burials, reburials, and cremations have been found. Often rocks or broken milling stones lie heaped up over the bodies. Grave goods were never elaborate or abundant, with shell beads and milling stones representing the most common accompaniments (Wallace 1978a).

It is possible that at the time of reburial, there was no fluid asphalt present at the surface. Disturbance of the late Pleistocene hardened asphaltic cap of the north vent by grave digging may have re-activated seepage of fresh asphalt which impregnated the remains.

Recognition of this occurrence as a formal reburial is not antithetical to the homicide theory. However, the purported trauma-induced cranial fractures are less convincing in x-rays and microscopic examination than in gross aspect. Some fractures do not appear in photographs taken in 1914 prior to restoration, and some apparent artifactual fractures have rounded rather than the expected sharp edges. Conversely, some of the non-artifactual fractures identified by Bromage and Shermis (1981) have sharper breaks than would be expected. Furthermore, fragments of the skull and mandible were drilled and wired together and missing parts were sculpted in with paper mache. Microscopic examination clearly shows that some fractures and junctions between bone and paper mache were sanded where necessary to make these contacts smooth. This has resulted in a rounded and misleading appearance of some fractures. Ideally, the skull fragments should be disassembled, cleaned thoroughly (i.e., of matrix, clay, latex, paper mache, glue, and wires) and the fractures examined in detail.

The organic content of bone is important in determining the fracturing characteristics. Fresh ("green") bone fractures in a different way than dry bone. Late Pleistocene bones from Rancho La Brea retain from one-sixth to four-fifths of their original collagen content (Ho 1965, 1966, 1967). A study of fracturing with bones from Rancho La Brea has not yet been addressed, thus, differences between fresh and fossil bone fractures are presently unknown for this deposit.

Despite a resemblance to cranial trauma, there is no evidence to suggest when this damage occurred or indeed if it resulted from traumatic insult. It is possible the damage occurred between the time of natural death and the time her remains were placed in the north vent. A temporary grave was usually covered with a cairn of large heavy rocks to discourage disinterment by carrion feeders such as grizzly bears. Also, grave digging and disinterment were most likely done with digging sticks and were likely shallow excavations. The potential for cranial damage by heavy rocks and digging sticks is very high. In addition, damage to the human cranium may have occurred *in situ* from stresses associated with pit wear, or even from the weight of the excavators standing above the skull on the plastic-consistency asphalt prior to its discovery. Bromage and Shermis (1981) suggest that after bludgeoning to death the body was thrown into a tar pit to conceal the deed. This is not calculated to have been an effective measure since evidence based on the insect assemblage at Rancho La Brea indicates that bodies of animals did not immediately sink but remained exposed at the surface for a minimum of five months (Stock 1956).

In a recent taphonomy paper concerning the myriad causes of bone breakage in a fossil thanatocoenosis, Walker (1980) warns that: "One hardly expects forensic scientists to know what fossils are really like, and to ask them what caused crushing of a skull is inviting an answer based only on analogies with their postmortem-room findings." It is not my intention to discredit the homicide theory which I was among the first to suggest (Reynolds 1968; Berger et al. 1971). I now find the evidence supporting cranial trauma inconclusive and subject to other interpretations. Viewed as a whole, this assemblage is best treated as a formal reburial.

Summary

The partial human skeleton discovered in 1914 in the north vent of Pit 10 at Rancho La Brea represents a female aborigine, probably Chumash. Radiocarbon dating of bone collagen indicates an age of 9000 ± 80 BP for this individual. Associated with the human were cranial remains of a domestic dog, referable on morphologic criteria to the Techichi, and a number of "killed" artifacts. Reassessment of all available data related to the human remains indicates this occurrence is a reburial rather than an accidental entrapment or the disposal of a homicide victim. The age determination of 9000 BP for the Techichi and the "killed" mano and shell ornaments (grave goods) is based on their association with the human remains. It is extremely unlikely that these three unique occurrences (*viz*, Techichi, "killed" artifacts, and human skeletal remains) are unrelated. A late Pleistocene asphalt pocket containing extinct mammals and birds occurred near the surface of the north vent. Radiocarbon dating of this component ($15,700 \pm 530$ BP) indicates no temporal association exists between this extinct fauna and the human reburial. The south vent of Pit 10 was of sub-Recent age (Radiocarbon date 5270 ± 155 BP) and contained no extinct mammals. The Pit 10 Techichi is perhaps the earliest example of domestic dog in California. Except for placement in asphalt, this reburial is consistent with the earliest known mortuary practices in California.

Acknowledgments

I am indebted to William A. Akersten, George T. Jefferson, Leslie F. Marcus,

Christopher A. Shaw for their comments and critical reading of the manuscript; Janet E. Helms for preparation of specimen LACMHC 6260; Rainer Berger and Richard Pardi for the radiocarbon dating; Mary Lorraine Romig for the final typing of the manuscript; William A. Akersten for the stereo-photography; and National Science Foundation Grant G. B. 5119 for partial support. This study was conducted at the George C. Page Museum.

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Accepted for publication 15 February 1984.

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Canine Fracture Avulsion in *Smilodon californicus*

Stewart Shermis

Abstract.—Canine fracture avulsion in *Smilodon californicus* by Stewart Shermis. Bull. Southern California Acad. Sci., 84(2):86-95, 1985. Seven crania of *Smilodon californicus* were analysed for at least one ante-mortem loss of a maxillary canine per cranium. Two crania demonstrated clear evidence of post-traumatic cortical inflammation, the root of one canine was displaced into the nasal cavity while another is still *in situ*. All evidenced more or less healing of the alveolar socket. Given the healed traumatic lesions in ribs and scapulae of *smilodon*, it points to a structurally weak tooth which was employed in both hard and soft tissue.

Injuries and diseases contracted by any vertebrate species may be descriptive of certain behavioral or ecological mechanisms influencing those animals. Perhaps the most telling of diseases are traumatic fractures, as they are always a faithful mirror of some environmental or behavioral stress. Regardless of species, a grouping of certain fractures or areas of fractures requires a reasonable explanation.

There is seldom any disagreement with overt signs of healed fractures; these often take standard appearances predicated upon bone biology or remodeling and mammalian anatomy and physiology. Their interpretation, however, is quite another matter. It is here that science gives way to art, as ethology is a young science and paleoethology is a highly speculative endeavor. Thus, while the conclusions of this paper appear wholly reasonable and predicated upon the best of evidence, they must necessarily be accepted with a measure of tentativeness.

Methodology and Results

The *Smilodon* skeletal material described below come from the Hancock Collection located in Hancock Park at the George C. Page Museum, Rancho La Brea, a branch of the Natural History Museum of Los Angeles County. In most instances, examination of the specimens included X-ray analysis as well as gross examination. The seven crania, 74 scapulae, and 112 ribs involved in this study were previously segregated by the Museum staff.

Each of the seven crania, LACMHC-417; 127; 154; 192; 461; 459; 237, exhibited the absence of a single canine lost antemortem. In all instances, the alveolus of that tooth had been to some extent resorbed (Fig. 1 and 2) with little or no indication of a root socket. This suggests that the tooth was lost at least a number of months, perhaps years before the animal died.

Two of these crania, LACMHC 2001-154 and LACMHC 2001-461, exhibit the usual characteristics of a low-grade cortical inflammation: a highly irregular surface with coarse, lacy, reactive bone. This further suggests that at some time subsequent to the avulsion fracture, a long standing inflammatory infection set in. The fracture was likely caused by a profound tearing or wrenching. Some areas of this cortical bone were pus producing as can be seen by the cloaca (Fig. 5) or

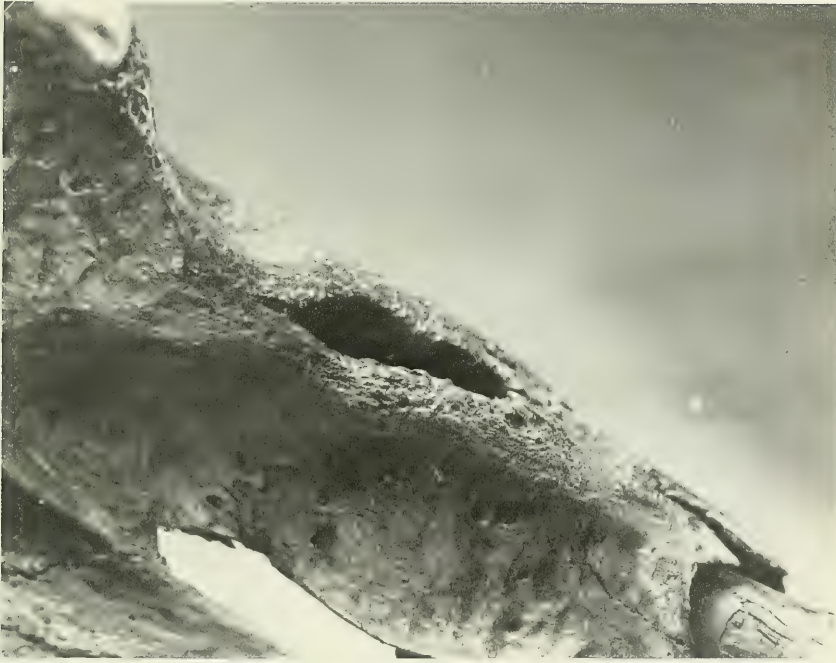


Fig. 1. A patent alveolar socket indicating a sabre lost antemortem. Surrounding alveolar tissue shows noticeable resorption while margins are constricted and remodeled. LACMHC 2001-154.

cloacae. These are conduits excavated through cortical bone by pus for the release of pus which was formed. That these features are indeed cloacae rather than focal pitwear is confirmed by the smoothly rounded margins, the direct consequence of the osteolytic action of pus. In three of the seven crania, near total resorption of the tooth root within the maxilla indicates long term absence of the canine either through non-formation, poor formation, or avulsion fracture; the cause is not clear. In one cranium (LACMHC 2001-192) the remnants of the root are clearly exposed in the left nasal cavity where the root came to rest after violent torque and avulsion (Fig. 3). In another LACMHC (2001-417), canine fragments can be seen through the cloacae in the buccal portion of the maxilla (Fig. 4).

With the loss of the canine, resorption of the alveolus produced obvious asymmetry of the splanchnocranium, noted also by Moodie (1929). This is reflected in both gross skeletal tissue and the scars for muscle attachment. To what extent this asymmetric atrophic degeneration presented survival stress is, of course, unknown. Inasmuch as *Smilodon* was likely a gregarious animal, (Gonyea 1976; Akersten, in prep.) the stress was probably minimal. That it was not a significant factor in survival can be seen in the long term survival of the animal after the avulsion fracture of the canine.

Discussion

The exaggerated size and particular architecture of the *Smilodon* saber predisposed the tooth to fracture when employed under extraordinary stress. The tooth is well imbedded in the maxilla and has a crown to root ratio of approximately



Fig. 2. Arrow points to alveolar bone scar which has completely fused after long-standing loss of right saber. Maxilla has undergone significant atrophic degeneration as a result of the loss of the tooth. LACMHC 2001-192.

3:2. It was this deeply anchored root which contributed to the powerful use of this canine as a true saber, a slashing as well as a puncturing weapon. The saber, described best by Merriam and Stock (1932), is most unlike the canine found in other living carnivores. Rather than being conical in shape, the tooth is approximately plano-convex with the more convex surface facing laterally. Some 13 cm in overall length, the recurved tooth tapers to a blunt point. The enamel on this canine is a millimeter or so thick; it amounts to little more than a thin slip of enamel covering the crown. Inasmuch as enamel is 96–98% inorganic salts while dentin is significantly softer, reduced amounts of enamel weakens a tooth under stress. Adding to the structural weakness of the tooth is a large pulp chamber seen in immature forms, in some cases amounting to 50% of the diameter of the tooth at a point where the crown meets the root. Thus, the *Smilodon* canine is long, largely composed of softer dentine, may possess a capacious pulp chamber and is relatively thin. On architectural grounds alone the tooth was vulnerable to torque and lateral stress. Were the saber employed only in soft tissue, it is likely that the tooth would sustain little trauma. The evidence, however, suggests that *Smilodon* thrust its canine into both hard and soft tissue of conspecifics and likely



Fig. 3. Arrow points to a fractured left saber root displaced into the nasal cavity as a consequence of an avulsion fracture of crown and part of root. Such displacement indicates very powerful rotational stress on tooth. LACMHC 2001-192.

prey animals. The evidence is in the form of those scars which occur after bone injury.

Bone injuries have been examined in the cranium and thorax of *Smilodon*. A penetration injury to the cranium has already been described (Miller 1980; Shermis, in press) and consists of a wound through the frontonasal bones, the outlines of which accommodate a saber with ease. Injury to the thorax is limited in this study to an analysis of the scapulae and ribs of *Smilodon*. It is believed that *Smilodon*, as with most other large cats, attacked conspecifics in the area of the neck. If healed wounds were to be observed they would be seen in these two kinds of bones. This idea was suggested to the author by a *Smilodon* rib on display at the Page Museum and described by Akersten (in prep.) showing the very tip of a saber imbedded in the bone.

Trauma to the 74 scapulae consist of three kinds of injuries, not necessarily exclusive. The myositis ossificans traumaticae are all raised lesions from the cortex of the bone and represent extravasated blood that lay close to the bone which was subsequently fibrosed and then calcified. These appear as raised asymmetrical lumps on the cortex of the bone, usually seen on the superior surface of the

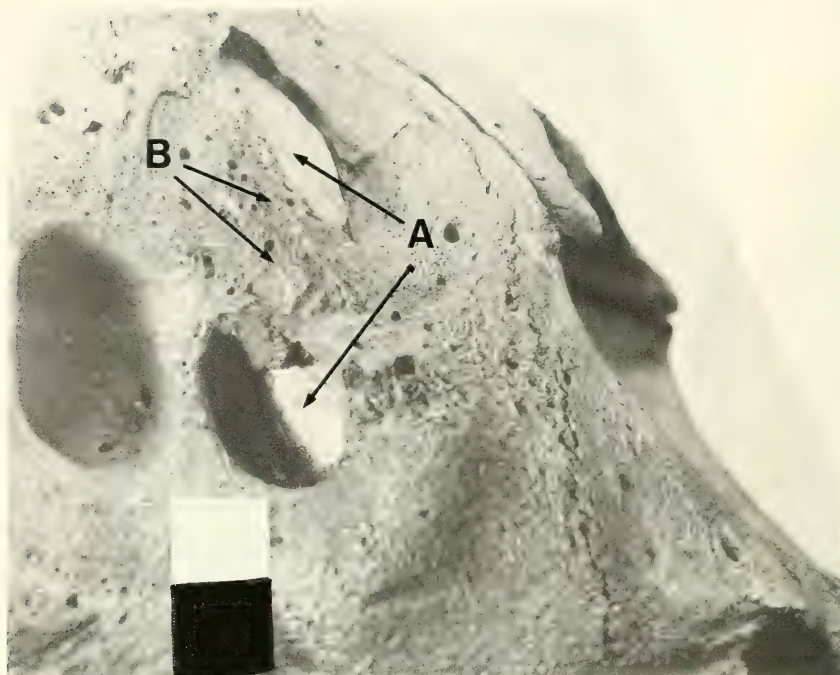


Fig. 4. *Smilodon* right maxilla. Arrows "A" point to the remnants of canine root which have remained after avulsion fracture. Roots appear through enlarged cloaca. Superior portion of maxilla has undergone atrophy as well as degeneration from osteitis, arrows "B." LACMHC 2001-417. Bar = 2 cm.



Fig. 5. Right maxilla illustrating the reactive bone of chronic osteitis subsequent to avulsion fracture. The large irregularly-shaped holes are cloacae through which pus was discharged from internal bone tissue. LACMHC 2001-154.

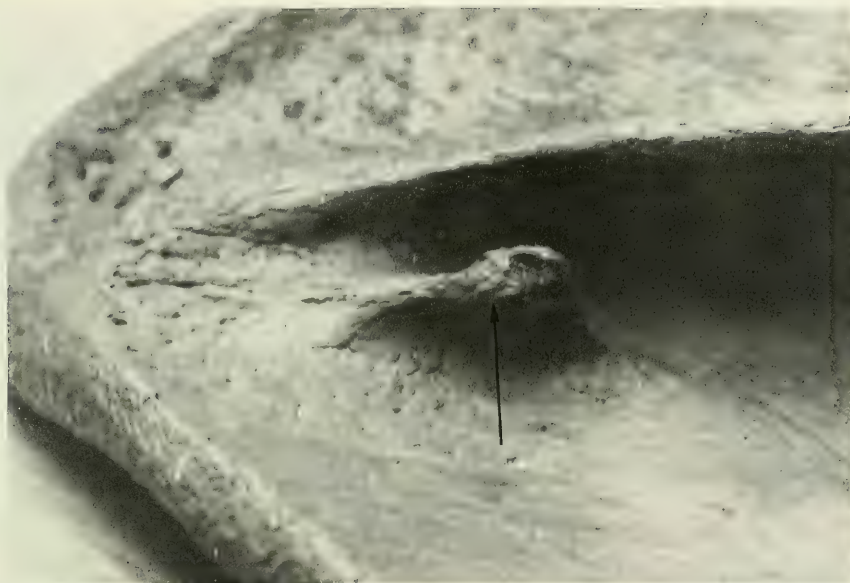


Fig. 6. Arrow points to an exostosis of a myositis ossificans traumatica near the base of the scapular spine. These arise from injury to or near the cortical surface. Their large incidence presupposes common, intense intraspecific combat. LACMHC K-139.

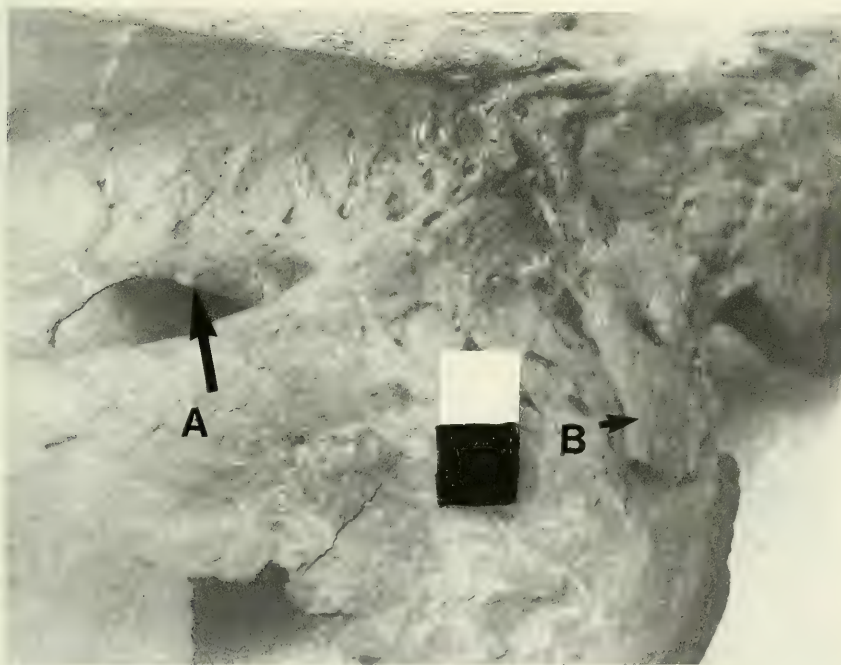


Fig. 7. Arrow "A" points to likely saber puncture wound near spine of scapula. Arrow "B" represents fracture at medial angle. Fractured area has displaced to a point medial to its original location. LACMHC K-107. Bar = 2 cm.

superspinous and infraspinous fossae (Fig. 6) and are commonly pedunculated. Fractures are limited to the blade of the scapula and frequently involve the spinous process. The fractures range in severity from minimal damage to the blade to considerable distortion of this structure. All fractures can be recognized by healing callus tissue in the vicinity of the original site of fracture which may extend well beyond it (Fig. 7). Puncture wounds of the blade may be either single or multiple, with single perforations predominating. The margins of the puncture wounds are generally symmetrical and gently rounded, (Figs. 7 and 8). These three types of traumas are distributed as follows:

TYPE	NUMBER	PERCENT
Myositis ossificans	41	55.5%
Traumatic fractures	17	22.9%
Puncture wounds	<u>16</u>	<u>21.6%</u>
	74	100.0%

Given the trauma to the scapulae, it is logical that the ribs would show similar evidence of injury. The pathology collection contains 112 ribs either nonspecifically traumatized or traumatically fractured. Twelve of the fractures represent non-union healing or pseudoarthroses. The distribution is as follows:



Fig. 8. Puncture fracture near the base of the spinous process. Perforation faithfully retains the shape of the canine tooth. Lesion is rounded indicating a fully healed wound. LACMHC D-13.

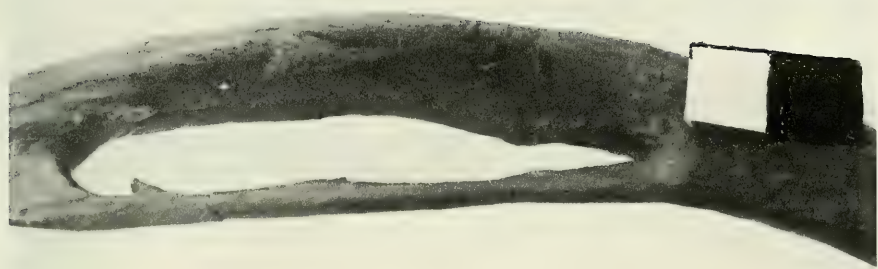


Fig. 9. *Smilodon* rib which had been longitudinally sliced likely by the shearing action of a saber. LACMHC 281. Bar = 2 cm.

TYPE	NUMBER	PERCENT
Healed fracture	73	65.2%
Non-healed fracture	12	10.7%
Traumatized	27	24.1%
	112	100.0%

It would be the height of folly to ascribe all the trauma to the scapulae and ribs as the consequence of intraspecific combat with the damage done by the sabers. It is likely, however, that a good number of these wounds were induced by *Smilodon* either by tooth or claw. It would be hard to imagine how the longitudinal fracture of the rib (Fig. 9) could have been caused by anything but a saber penetration. In sum, the evidence suggests that *Smilodon* did insert into both hard and soft tissue alike. It is believed that the penetration into bone with subsequent lateral stress caused the avulsion fractures. It must be recalled that the observed trauma is limited to *Smilodon*. The exact nature of the pattern of trauma to its prey is unknown and likely unknowable: healed lesions of prey are not likely to be found in large numbers.

The precise behavioral and anatomical mechanisms which were the proximate cause of these fractures can only be deduced, but from good evidence. Commensurate with a tooth evolved for deep penetration was the musculature necessary for strong depression of the head. By all accounts (Merriam and Stock 1932; Matthew 1910; Akersten, in prep.) the craniocervical region was possessed of bone structures which reflect not only powerful neck depressing musculature but those involved in rotation. This is reasonable as the well-developed atlantomastoid muscular complex likely served both functions. Both depression and rotation of the head are a highly coordinated activity and those muscles which serve the one function may well be involved in the other. By whatever measure, the craniocervical bone development of *Smilodon* is on a par with the highly specialized canine teeth.

An element, though not a particularly crucial one, in the discussion is the structural anatomy of the alveolar bone housing these maxillary canines. Whereas the alveolar bone of the incisor and premolar teeth tend to be compact and relatively thick, the bone encasing the roots of the sabers is thin and attenuated along the lateral margins as it approaches the gumline. At this point it provides meager structural support for so massive a tooth under lateral stress. If the tooth were limited to soft tissue penetration only as cogently argued by Akersten (in prep.), there would be minor stress placed upon the canine tooth and buccal plate. The evidence, however, suggests otherwise.

There are animals with outsized canines whose employment has little to do with predation. The gorilla, for example, whose canines reach an impressive length, restrict their use to displays, defensive charges and the mastication of coarse vegetation (Schaller 1963). Carnivores, on the other hand, employ their canines for defense and offense involving tissue tearing. Felids typically attack the neck/head region, but in the fury of the moment their aim may well be any place in the anterior part of the body. A saber deeply penetrating a scapula or some other hard tissue and then sharply rotated might well shear off. A saber could conceivably fracture if imbedded into nonvital, soft muscle tissue with much movement on the part of the prey. Given the anatomic weakness of this oversized tooth, the finding of an occasional avulsion fracture is not to be wondered at.

Conclusion

The *Smilodon* saber is long, narrow, composed largely of the softer dentine, and possesses a capacious pulp chamber in immature forms. The ability of the animal to sink this tooth deeply into its prey was enhanced by powerful muscles of depression and rotation. Given the number of healed traumas to the thorax of conspecifics, it is to be believed that *Smilodon* employed these teeth in both hard and soft tissue. The combination of the above factors may well account for the missing canines on the seven crania examined and a number of postcranial healed lesions.

Acknowledgments

I should like to extend my sincerest thanks to the staff and management of the George C. Page Museum for allowing me to delve through their vast collections and upset their ordered routine. My special thanks extends to Christopher A. Shaw and William Akersten who provided helpful criticism.

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Accepted for publication 5 July 1984.

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Sexual Dimorphism of the Upper Jaw in *Gillichthys mirabilis*

C. Ben Crabtree

Abstract.—Sexual dimorphism of the upper jaw in *Gillichthys mirabilis* by C. Ben Crabtree. *Bull. Southern California Acad. Sci.*, 84(2):96–103, 1985. *Gillichthys mirabilis*, the longjaw mudsucker, is easily recognized because of the posteriorly elongated maxillaries. Although expressed in both males and females, this feature is more conspicuous in the males. Simple linear regressions of upper jaw length indicate statistically significant differences in the development of this feature between the sexes. Growth of the maxillaries is relatively constant in young individuals, but the rate of growth increases with maturation. In both sexes, the rate of increase in the length of the upper jaw accelerates with age, but to a greater degree in the males, resulting in a sexually dimorphic character. Quantitative description of the ontogenetic development of this feature is best described by a nonlinear power function. Based on this investigation, the description of allometric growth may be more accurately addressed using nonlinear regression analysis rather than the standard linear or log-linear regression procedures. The dimorphism in this feature has little apparent relevance to diet. Although the females analyzed contained a higher proportion of the small prey item size class than the males, differences between the sexes were nonsignificant. The primary function of this feature appears to be its use in sexual behavior: display and territorial defense.

Gillichthys mirabilis, one of the largest gobiid fishes of the northeastern Pacific, is a major component of the ichthyofauna of bays and lagoons of southern California and the west coast of Baja California north of Cabo San Lucas (Barlow 1961a, 1963). *G. mirabilis* is also found in the Gulf of California along the east coast of Baja California south to Mulege and south to Bahia Agiabampo on the west coast of mainland Mexico (Barlow 1961a). In addition, this species has been introduced into the Salton Sea (Walker et al. 1961).

In the bays and lagoons, *Gillichthys mirabilis* commonly resides in burrows in the muddy banks above the water level during low tide (Barnhardt 1936; Barlow 1961a) or may occasionally be found exposed, moving between pools in mudflat areas (Moyle and Cech 1982, pers. obs.). During periods of exposure, this species relies on aerial respiration (Todd and Ebeling 1966; Barlow 1961b). During high tide intervals, the fish moves out into the channels and sloughs to feed, primarily on crustaceans and small fishes.

As the common name of *G. mirabilis* implies (the longjaw mudsucker), a conspicuous feature of the external morphology of this species is the posterior extension of the maxillaries. Although both males and females exhibit this characteristic, the males display a more posteriorly elongated upper jaw than the females (Fig. 1). The upper jaw length was among the morphometric features analyzed by Barlow (1961a) in the redescription of the two species of *Gillichthys* in the Gulf of California. Of the specimens analyzed by Barlow, the measures

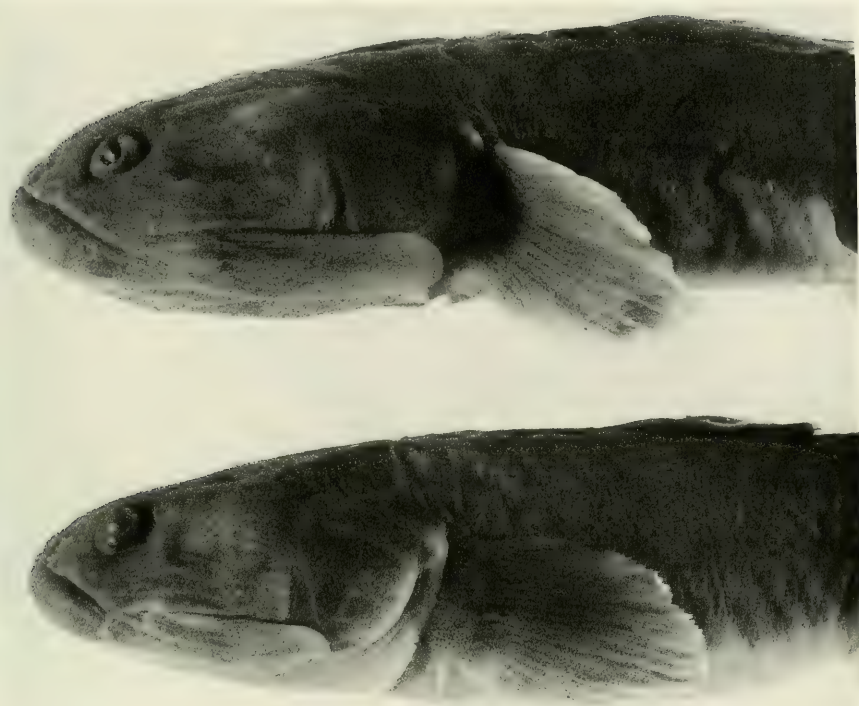


Fig. 1. Male (above; 116.55 mm SL) and female (below; 114.75 mm SL) specimens of *Gillichthys mirabilis* exhibiting sexual dimorphism of upper jaw length.

obtained for the males and females obviously differed, although no statistical criterion was employed to distinguish the sexes or to describe the development of this feature.

The sexual dimorphism in upper jaw length in this fish raises questions concerning the ontogenetic development and the function of this feature. This investigation centers on a statistical analysis of the upper jaw length between the sexes and a description of the ontogenetic development of this feature by linear and nonlinear regression analyses. The possible function of this dimorphic feature is also addressed, including possible contributions to differential prey size items taken and its role in sexual behavior.

Materials and Methods

Gillichthys mirabilis were collected at Ballona Marsh in southern California using minnow traps and seines. The specimens were fixed in 10% formalin upon capture. Sex determination was based on the presence or absence of seminal vesicles as described by Weisel (1949). This method did not allow sexing of specimens less than 30 millimeters standard length (hereafter referred to as juveniles).

For each specimen, standard length and upper jaw length were measured (following Hubbs and Lagler 1949). Plots of upper jaw length against standard length were used in the analysis of the measures. Analysis of the numerical data, within

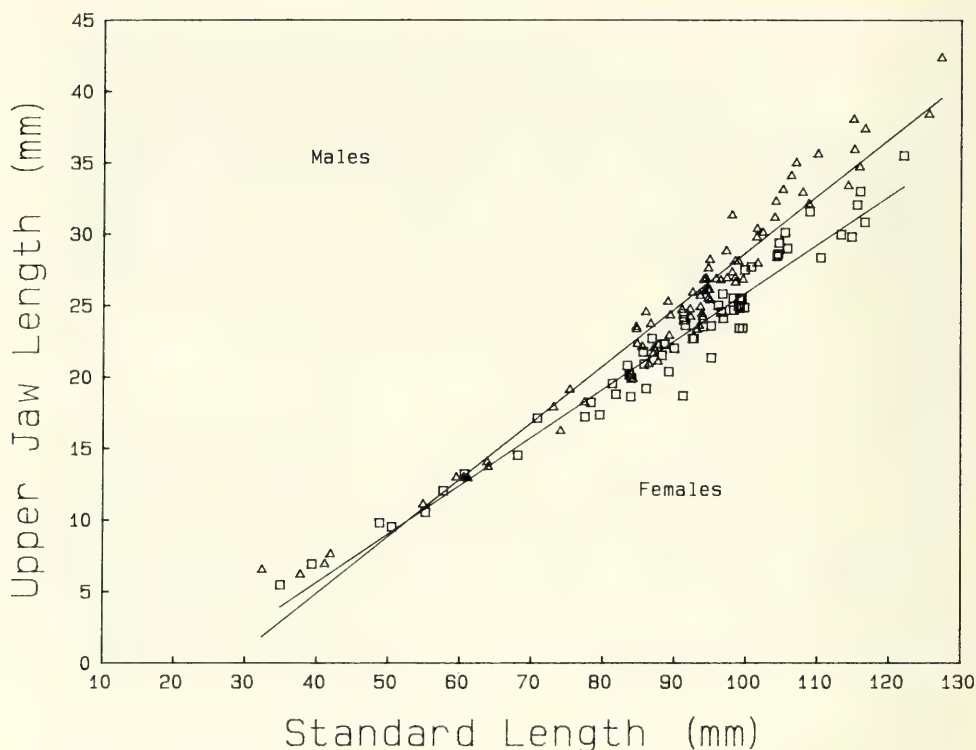


Fig. 2. Plot of the individual specimens and the linear regression lines for the males (Δ) and females ($\square$).

and between classes of individuals (males, females, and juveniles), was performed using simple linear regression (Zar 1974) and the nonlinear regression curve fitting method of Marquardt (1963). Assessment of the descriptive potential for the two types of regression was based on qualitative comparison of the respective correlation coefficients.

To test for potential differences in the size of prey items taken by individuals, the contents of the entire alimentary canal of five males and five females, of the same approximate size (114.90 ± 1.65 mm standard length), were removed and identified. The contents were divided into three separate size classes based on the maximum dimension of the prey item (<5 mm; 5–10 mm; and >10 mm). Volumetric measures were taken for each of the three prey item size classes and analyzed statistically [contingency chi-square test (Crow 1982)] to test for significant differences between the sexes for the different size classes of prey items. For each specimen dissected for the gut content analysis, the tip of the snout to the angle of the jaw was measured to obtain an estimate of the maximum possible gape for comparison of the sexes [Student's t -test (Hays 1981)].

Results

The analyses using simple linear regression are shown in Figs. 2 and 3. Fig. 2 is a plot of the males and females with their respective regression lines. The r^2 values (and regression formulae) obtained for the regressions of the males and

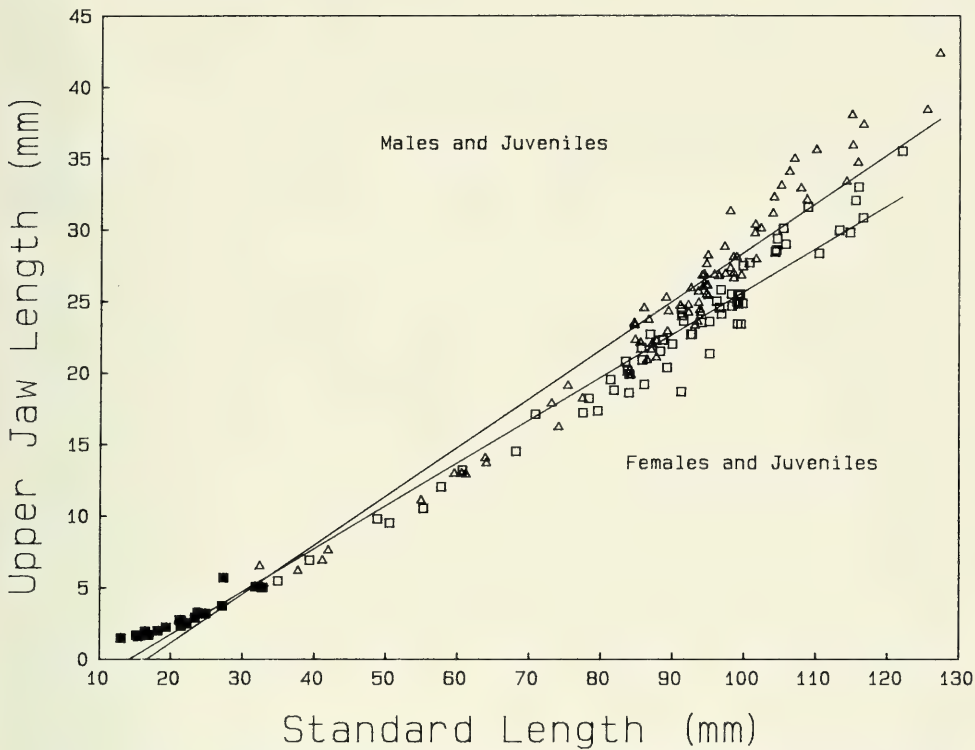


Fig. 3. Joint plot of the male/juvenile (Δ) and the female/juvenile ($\square$) specimens with the corresponding linear regression lines (juveniles denoted by a $\blacksquare$).

females are $0.953 [Y = -11.012 + (0.397)X]$ and $0.955 [Y = -7.812 + (0.338)X]$, respectively. Statistical comparison of the slopes of the male and female linear regressions indicate significant differences ($P < 0.05$). Fig. 3 represents a joint plot of the males/juveniles and the females/juveniles. The r^2 values (and regression formulae) for these data are $0.972 [Y = -5.664 + (0.341)X]$ for the male/juvenile plot and $0.981 [Y = -4.241 + (0.299)X]$ for the female/juvenile plot.

Three nonlinear functions were fit to the male/juvenile and female/juvenile data: logarithmic; exponential; and power functions. Of these functions, the best fit was derived from a power function of the form $y = ax^b$. The results of the nonlinear regression analysis for the plots of these data are shown in Fig. 4. The r^2 values for the nonlinear regressions are 0.994 for the male/juvenile plot and 0.994 for the female/juvenile plot. The regression formulae of the power functions for the male/juvenile and female/juvenile data are $Y = 0.025 (X^{1.528})$ and $Y = 0.030 (X^{1.466})$, respectively.

Table 1 shows the volumetric measures for the gut contents of the males and females investigated. The prey items of the specimens examined consisted of detritus, grapsid crabs and fish remains (identification unknown). The contingency chi-square analysis indicate nonsignificant differences in the relative amounts of the prey item size classes between the males and females ($P > 0.05$). The results of the statistical analysis of the snout to the angle of the jaw also indicate nonsignificant differences between the sexes ($P > 0.05$).

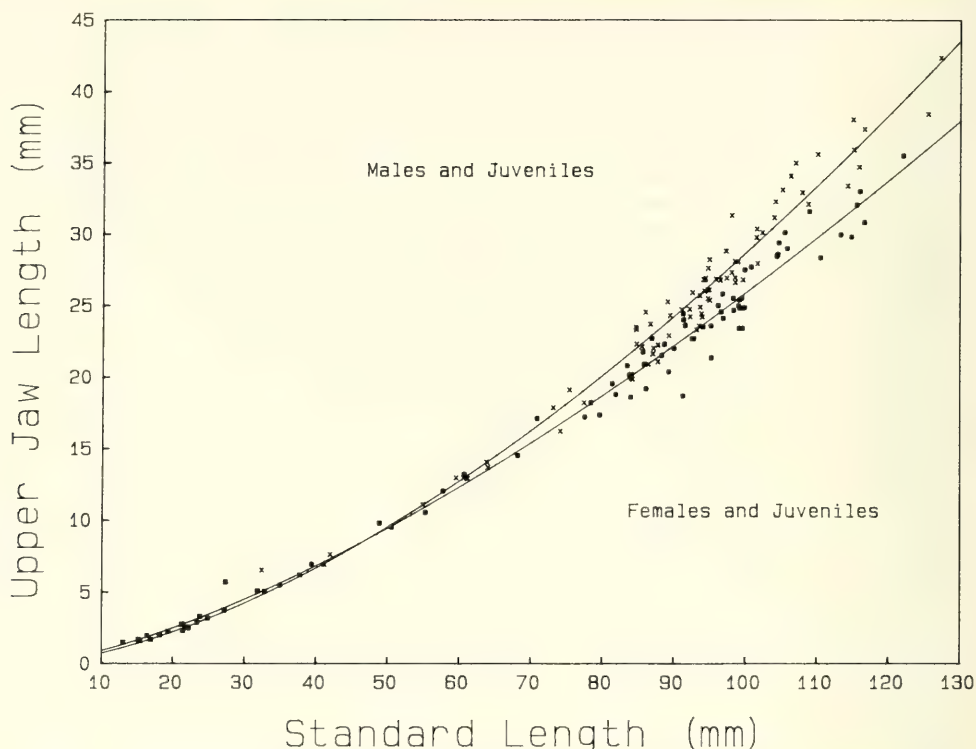


Fig. 4. Joint plot of the male/juvenile (x) and the female/juvenile (o) specimens with the corresponding nonlinear regression lines (juveniles denoted by a ■).

Discussion

Ontogenetic development of the upper jaw.—Throughout the ontogenetic development of an organism, many features of organisms grow at different rates (Pimentel 1979). If different morphological features grow at different rates, or if the rate of relative growth changes with the age of an individual, description of the growth pattern may be more accurately represented by a nonlinear equation than a linear equation.

The linear regression analyses of the males and females exhibit significantly different slopes between the classes. From Figs. 2 and 3, it is evident that the allometric increase in the upper jaw length is relatively constant in small individuals (<30 mm standard length). At the point during development when the reproductive structures are recognizable, up to the adult size, the rate of increase in relative upper jaw length appears to accelerate, but differentially in the males and females. The linear regression analyses indicate that the accelerated rate of allometric growth is greater in the males than in the females.

An alternative quantitative method to describe the ontogenetic development of the upper jaw is a nonlinear regression analysis. The nonlinear regression analysis actually yielded a higher r^2 than the linear analysis. These results are interesting for two reasons: first, quantitative description of the development of the upper jaw in *Gillichthys mirabilis* is more closely described by a nonlinear

Table 1. Total volumetric measures (cc $\times$ 10) of the gut contents of five male and five female *Gillichthys mirabilis* for three prey item size classes.

Sex	Prey item size class		
	<5 mm	5–10 mm	>10 mm
Male	9.0	1.5	15.0
Female	12.0	1.0	10.5

function than a linear function; and second, when a nonlinear function is used to describe the development of this feature, the joint plots *both* yield high r^2 values. Qualitatively, the allometric increase in upper jaw length is slow in small individuals and with maturation, the lengthening accelerates, but to a greater degree in the males resulting in more posteriorly elongated maxillaries in the males.

Functional significance.—The investigation of the gut contents revealed no significant differences between the males and females. As evidenced from the gut content analysis, feeding in this species appears to be by swallowing its prey whole (the large prey items consisted primarily of whole gapsid crabs). Given that the upper jaw of the males is longer than that in females, the elongated maxillaries *may* enable the males to open their mouths wider than the females. Thus, *a priori*, we may expect the males to take larger prey items than the females of the same size. This was found to be the case; the female specimens contained relatively more prey items of the small size class than the males yet the sexes did not differ significantly in gape length. Because the sexes differ significantly in upper jaw length, but not in gape length, the elongated upper jaw in the males may serve some function other than feeding. Based on the sample size, however, it is difficult to conclusively discount this possible function.

The presence of a sexually dimorphic feature in organisms often indicates that the feature may be used in sexual behavior, in the form of territorial defense or sexual displays (Wilson 1980; Immelman 1980). The function of the posteriorly elongated maxillaries in male *G. mirabilis* was reported by Weisel (1947). During territorial defense, males will drop the lower jaw which (via ligamentous connections) results in a lateral protrusion of the posterior ends of the maxillaries. The highly vascularized membrane that extends from the maxillaries to the dentaries is stretched to form a structure that is "sail-like on either side of the head" (Weisel 1947). Males use this display to displace intruding males from their breeding territory. The anterior portion of the maxilla is fixed relatively tightly via a connection with the nasal region of the skull. The posterior end of the maxilla however hangs free except for a dorso-medial ligamentous connection to the dentary in the lower jaw. By dropping the lower jaw, the maxilla is rotated resulting in a lateral protrusion of the posterior end of the maxilla.

The lateral protrusion of the maxillaries presumably functions to make the male look as large as possible, therefore frightening off other males. This specific type of display, the enlargement of the head region, has been documented in many fishes (Miller 1963; Adler 1975; Fryer and Iles 1972; Marler 1968). A startling convergence to the pattern observed in *G. mirabilis* has been described in a clinid, *Neoclinus blanchardi* (Feder et al. 1974). The latter species is also equipped with posteriorly elongated maxillaries that also function in territorial defense. This

species also exhibits this ballooning effect of the maxillary membranes. Thus, the flaring of the opercular flaps in many cichlids and sunfish (Fryer and Iles 1972; Miller 1963) and the "ballooning" of the maxillary membranes in *Neoclinus blanchardi* and *Gillichthys mirabilis* both function in the display of an enlarged head in intraspecific and interspecific confrontations.

Another possible function for the ballooning effect of the maxillary membranes may be respiratory as suggested by Weisel (1947). However the evidence presented by Todd and Ebeling (1966) indicates that this function is auxiliary at best. The primary surface of gas exchange used in aerial respiration by *G. mirabilis* is the bucco-pharyngeal region.

In summary, the posteriorly elongated upper jaw in *G. mirabilis* functions primarily in territorial behavior and perhaps to a lesser degree in sexual display. The greatly elongated maxillaries in the males enable them to flare the maxillary membranes in the defense of a breeding territory. The ontogenetic development of this feature is best described by a power function in both the males and females, although the rate of allometric growth differs between the two sexes. This study emphasizes the requirement for investigation of methods other than simple linear functions for the quantitative description of the ontogenetic development of allometrically growing features. Although log-linear analyses often closer approximate the development of these features, alternative analytical functions may be more informative in the description of allometric growth in organisms.

Acknowledgments

This research was supported in part by the University of California (UCLA), Department of Biology Organismal Fund. Permission to collect specimens for this study was granted by the State of California, permit #2104. I would like to gratefully acknowledge the field assistance of C. Swift and the helpful discussions of R. Lea, J. Peterson, and J. Baumer. B. Walker, A. Ebeling, and T. Shelly kindly reviewed the manuscript and provided helpful comments. D. Buth's guidance and assistance in this study is greatly appreciated.

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Accepted for publication 30 March 1984.

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A New Species of *Asymmetrione* (Isopoda: Bopyridae) Infesting the Hermit Crab *Isocheles pilosus* (Holmes) in Southern California

John C. Markham

Abstract.—A new species of *Asymmetrione* (Isopoda: Bopyridae) infesting the hermit crab *Isocheles pilosus* (Holmes) in southern California by John C. Markham. *Bull. Southern California Acad. Sci.*, 84(2):104–108, 1985. The new species *Asymmetrione ambodistorta* is described and figured. It belongs among those species of *Asymmetrione* whose females are distorted relatively little, but is unique in the genus for having females distorted in both directions, hence its specific name. *Asymmetrione ambodistorta* is the first species of *Asymmetrione* to be described from the eastern Pacific Ocean.

Recently, Dr. F. G. Hochberg of the Santa Barbara Museum of Natural History (SBMNH) made available for study several specimens of bopyrid isopods housed in the collection of that museum. One series of four pairs is of particular interest in that it represents a new species of the genus *Asymmetrione*, the first such available for description from the eastern Pacific, the first such known to occur in both dextral and sinistral forms, and the first bopyrid of any genus recorded as a parasite of a species of the diogenid hermit crab genus *Isocheles*.

Asymmetrione ambodistorta n. sp.

Figures 1, 2

Material examined.—One female, holotype, SBMNH 33893; one male, allotype, SBMNH 33894, three females, three males, paratypes, SBMNH 33895. Infesting *Isocheles pilosus* (Holmes) (Anomura: Diogenidae), collected and determined by Andrea Braly, Newport Beach, Corona del Mar State Beach, California, depth ca. 3 m, 2 June 1982.

Description.—HOLOTYPE, female (Fig. 1). Length 5.42 mm, maximal width 3.56 mm, head length 1.44 mm, head width 1.44 mm, pleon length 1.29 mm. Body distortion 30°, sinistral. All body regions and segments distinct (Fig. 1A, B).

Head subcircular: Large frontal lamina irregularly four-lobed, extending far out from dorsal surface and beyond both sides of head. Antennae (Fig. 1C, D) well developed and evidently nonsetose, first of three articles, second of five, each article successively smaller proximally. Eyes absent. Posteroventral border (Fig. 1E) with lateral projection and irregularly shaped and toothed lobes on each side. Maxilliped (Fig. 1F, G) subelliptical, completely lacking palp and with only tiny nonextending spur.

Pereomeres irregularly shaped both laterally and transversely; small faint indentations on both sides of dorsal surfaces of first five pereomeres; coxal plates prominent on both sides of pereomeres 1–4; sides of pereomeres 5–7 on convex side produced into separated slender points sharply reflexed back over dorsal

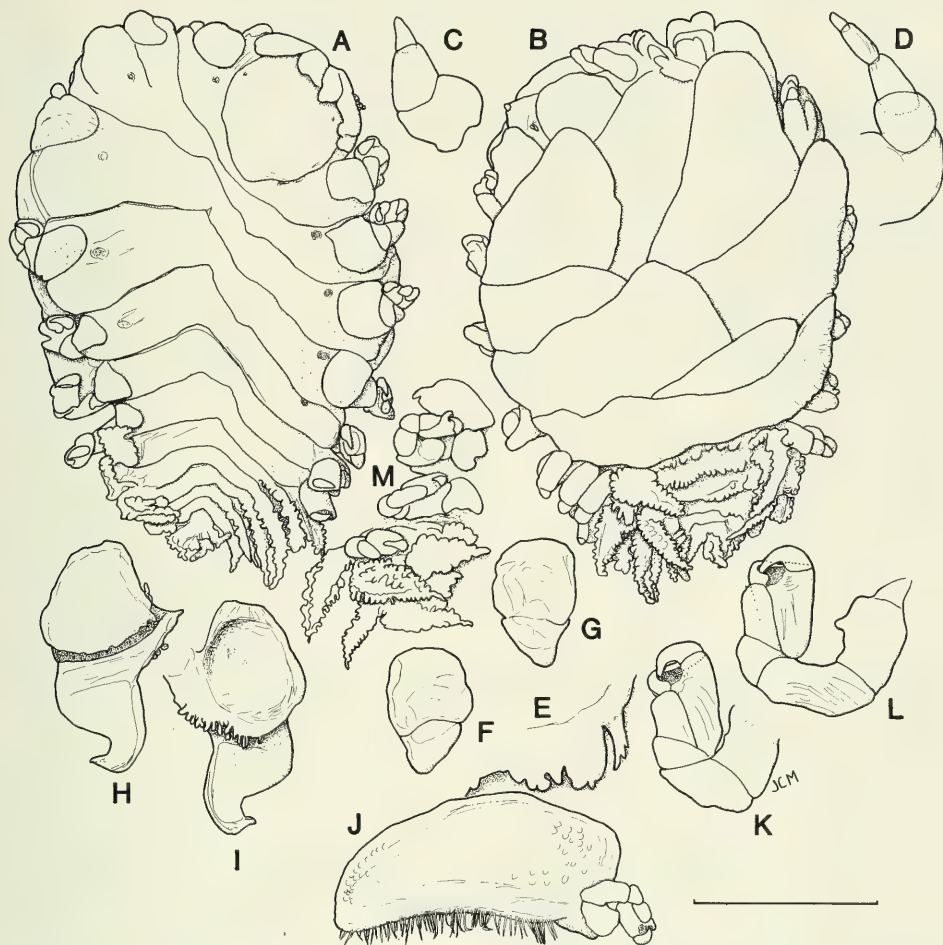


Fig. 1. *Asymmetrione ambodistorta* n. sp., holotype, female: A. dorsal; B. ventral; C. right antenna 1; D. right antenna 2; E. left posteroventral border of head; F. left maxilliped external; G. same, internal; H. left oostegite 1, external; I. same, internal; J. right oostegite 5; K. left pereopod 1; L. left pereopod 7; M. left pereopods 5-7, pleopods 1, 2, lateral view; Scale: 2.0 mm for A, B, F-J, M; 1.0 mm for E, K, L; 0.55 mm for C, D.

surfaces (Fig. 1A, M). Oostegites completely enclosing brood pouch; oostegite 1 (Fig. 1H, I) nearly twice as long as broad, ending in sharply curved falcate point; outer groove deep and conspicuous, inner ridge bearing many slender lobes. Oostegite 5 (Fig. 1J) subrectangular, with partly tuberculate surface and dense fringe of posterior setae. Pereopods (Fig. 1K, L) all of same structure, somewhat larger posteriorly, especially on concave side; all with deep propodal sockets to receive dactyl tips; bases variously carinate.

Pleomeres all chevron-shaped dorsally, their convex margins forward; posterior margins of most pleomeres scalloped ventrally. Each side of pleomeres 1-5 produced into dentate-margined lanceolate lateral plate and bearing similarly biramous pleopods (Fig. 1M). Pair of similar biramous uropods on pleomere 6. Mid-

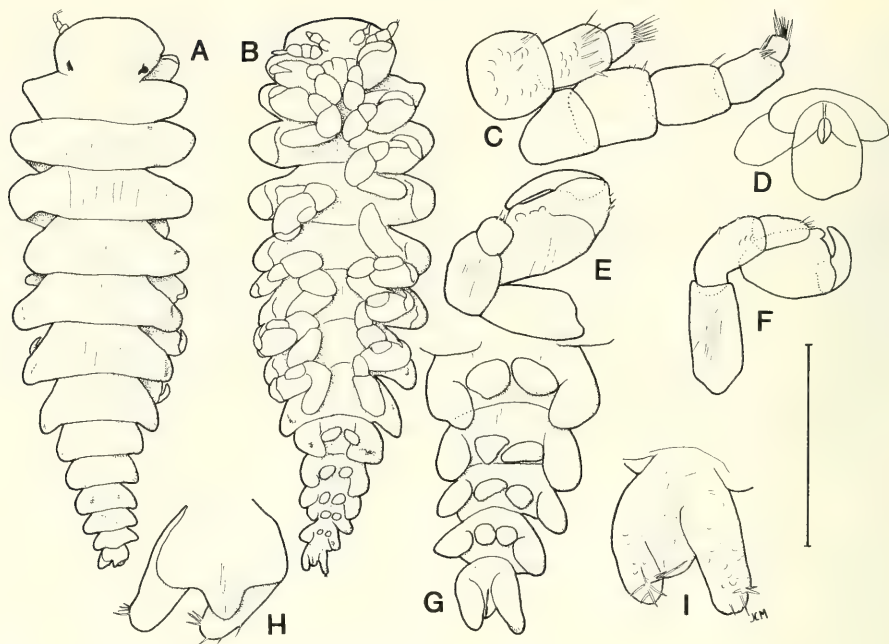


Fig. 2. *Asymmetrione ambodistorta* n. sp., allotype, male: A. dorsal; B. ventral; C. left antennae; D. mouth; E. left pereopod 1; F. left pereopod 7; G. pleon, ventral; H. last pleomere, dorsal; I. same, ventral; Scale: 1.0 mm for A, B; 0.4 mm for E, G; 0.2 mm for C, D, H, I.

ventral region of pleon not covered by appendages, serving as area of attachment for male.

ALLOTYPE, male (Fig. 2): Length 2.76 mm, maximal width 0.91 mm, head length 0.34 mm, head width 0.55 mm, pleon length 0.75 mm. Head and pereon dorsally fused, but all body regions and segments otherwise distinct (Fig. 2A, B). Some small pigment spots near sides of dorsal surfaces of several segments.

Head transversely oval, almost straight across front. Eyes small and dark, near posterolateral margins. Antennae (Fig. 2C) of three and five articles, respectively, each with many setae distally and some setae on nearly all other articles. Mouth (Fig. 2D) reduced.

Pereon broadest, but not markedly so, across pereomeres 2 and 3, though pereomeres 6 and 7 notably narrower than preceding ones. All pereomeres broadest posteriorly, tapering forward to leave lateral notches along both sides of body. Pereopods all of about same size but propodi and dactyli of first two pairs proportionately larger than others (Fig. 2E, F); merus and ischium of each evidently fused, as each pereopod of only five articles; carpus of each distally setose, and some setae also scattered elsewhere; surface of propodus of first pereopod (Fig. 2E) with aligned tubercles forming groove to receive dactylus; most propodi obliquely ridged near distal ends.

Pleon evenly tapered posteriorly, pleomeres similar in shape to pereomeres but much narrower. Lateral margins of all pleomeres sharply reflexed laterally and posteriorly (Fig. 2G). Five pairs of flaplike pleopods extending slightly from pleomeral surfaces (Fig. 2G). Final (sixth) pleomere (Fig. 2H, I) extended midposter-

iorly into anal cone and produced ventrally into large extended uropods, each with rosette of setae positioned subdistally.

PARATYPES, females: Two sinistral, one dextral. Lengths 4.32 to 5.08 mm. Distortion up to 50°. One maxilliped with slightly more extended spur. Most first oostegites with fewer and larger lobes on internal ridges; some fifth oostegites more pointed and less tuberculate. Appendages of one pleon difficult to interpret, bunched together.

PARATYPES, males: Length 2.40 to 2.64 mm, widths 0.82 to 0.92 mm. No noteworthy structural differences from allotype, but one specimen with abundant dorsolateral pigmentation.

Etymology.—The name *ambodistorta* meaning “both distorted” has been selected to refer to the occurrence of both dextral and sinistral forms in the females of this species, a situation otherwise unknown in the genus *Asymmetrione*.

Discussion

The genus *Asymmetrione* was established by Codreanu, Codreanu, and Pike (1965) to contain a Japanese hermit-crab infesting parasite originally described as *Pseudione asymmetrica* by Shiino (1933) and a closely similar species from the Red Sea. Bourdon (1968) created the genus *Megachelione* for a new species in the western Mediterranean, *M. foresti*, which is similar to other species of *Asymmetrione* but its female is much less distorted. At the same time, Bourdon (1968) described another species which he assigned to *Asymmetrione*. Markham (1975) described two western Atlantic species, incorporated *Megachelione* into *Asymmetrione*, and reviewed the genus *Asymmetrione*, then known to contain six described and two undescribed species. Bourdon (1976) described another species and further reviewed the genus in a paper prepared too early for a consideration of the combination of genera. Markham (1975) noted that all of the highly distorted females (belonging to *Asymmetrione*, s. s.) are dextral or bent so that their right sides are the longer (=“convex”) and occupying the right gill chambers of their hosts. The less distorted females (of the *Megachelione* type) are all sinistral. Aside from the direction and amount of distortion of their females, all species seem clearly assignable to a single genus. Bourdon (1976), while not considering whether *Megachelione* belongs in *Asymmetrione*, did recognize that all of the highly distorted (typically to 100°) females were known to be dextral and designated their species “*Asymmetrione dextres*.” Both dextral and sinistral forms are common within the Bopyridae, and in most species both forms, as mirror images, occur in about equal numbers. Only in a very few cases are species known exclusively in one form or the other.

Asymmetrione ambodistorta is clearly one of the less distorted species of the genus. As its name indicates, it occurs in both forms, a situation unique for any species of *Asymmetrione*, three females being sinistral and one dextral. It illustrates well all of the characters of the genus: female with very prominent lobate frontal lamina, large pereopodal propodi with “sockets” for dactyli, first oostegites with sharply tapered point and lobed internal ridge and biramous lanceolate pleopods and uropods; male long and slender with head usually dorsally fused with pereon, all segments set apart laterally, flaplike pleopods and large extended posterior lobes or uropods. The female of *A. ambodistorta* is relatively little distorted and mainly sinistral. These characters ally it with two other species of *Asymmetrione*,

namely *A. foresti* (Bourdon, 1968) and *A. desultor* Markham, 1975. Both sexes are most similar to those of *A. foresti*, a parasite of the diogenid hermit crab *Paguristes oculatus* Fabricius in the northwestern Mediterranean. The female of *A. ambodistorta* is different from that of *A. foresti* in being more distorted, having nontuberculate pereopods and having tuberculate margins on its pleonal appendages. The male of *A. ambodistorta*, in contrast with that of *A. foresti*, has five articles in its second antenna rather than seven, a tapered rather than nearly straight-sided pleon and relatively smaller pleomeres. The female of *A. ambodistorta* differs from all other described species of *Asymmetrione* in having depressions on the dorsolateral regions of most pereomeres and reflexed points on the convex sides of pereomeres 5 and 7. All other males of *Asymmetrione* have variously produced posterior extensions on the posterior margin of the final pleomere, which have not been interpreted as uropods; uniquely in males of *A. ambodistorta*, these projections are distinctly set off from the last pleomere, at least in dorsal view; therefore, they are here regarded as uropods.

In an earlier publication (Markham, 1975) I reported the discovery of a badly damaged female of an evidently undescribed species of *Asymmetrione* which had come from the Pacific coast of Costa Rica. That species remains undescribed, but because it is a highly distorted one, it cannot be the same as *A. ambodistorta*. Its recorded host, "*Clibanarius* sp.," could be any diogenid hermit crab found in the area.

This is the first record of a bopyrid infesting a species of *Isocheles*. Like each of the other species of *Asymmetrione*, except *A. desultor* Markham (1975) a parasite of four western Atlantic pagurids, *A. ambodistorta* is only known from a single species of diogenid hermit crab.

Acknowledgments

Thanks are extended to Dr. F. G. Hochberg for furnishing the material and making comments on the manuscript, and to Mrs. W. A. Markham for making facilities available at the Arch Cape Marine Laboratory, from which this is publication number 8.

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Accepted for publication 30 March 1984.

Arch Cape Marine Laboratory, Arch Cape, Oregon 97102.

Research Note

Crab Predation on Intertidal Populations of the Urchin *Strongylocentrotus purpuratus*

Purple sea urchins (*Strongylocentrotus purpuratus*) are abundant and important members of subtidal communities in California (North 1976). Nevertheless, they are often absent or present in low numbers in adjacent intertidal areas. Their absence or low densities in rocky intertidal communities is often regarded as a result of human predation (MacGinitie and MacGinitie 1968; Ricketts and Calvin 1968). This idea is indirectly supported by the occurrence of large intertidal populations in areas with limited human activities (e.g., marine reserves, wave-swept rocky reefs, offshore islands).

Besides humans, intertidal populations are preyed upon by Black Oystercatchers (*Haematopus bachmani*), and sea stars including *Dermasterias imbricata*, *Pisaster ochraceus*, *Pycnopodia helianthoides*. None of these predators (with the exception of *P. helianthoides*), however, decimate populations to the extent that human predation does, clearing entire tidepools and rocky reefs of urchins. *P. helianthoides* has been observed to "stampede" intertidal populations of *S. purpuratus* that are not in burrows and thus can clear a large area or tidepool (Mauzey, Birkeland, and Dayton 1968; Paine and Vadas 1969; Dayton 1975).

Intertidal populations of *S. purpuratus* can also undergo localized mass mortalities as a result of a yet undetermined disease that denudes the test of spines and epidermis, and may ultimately produce lesions throughout the test (Pearse, Costa, Yellin, and Agegian 1977). Although this disease has been previously associated with subtidal populations of the larger *Strongylocentrotus franciscanus*, a mass mortality of intertidal *S. purpuratus* occurred near Sunset Bay, Oregon during the summer of 1978 (J. T. Carlton, pers. comm.).

During intertidal studies on San Nicolas Island, Ventura County, California (39°16'N, 119°30'W) a previously unreported predator was observed clearing tidepools of urchins. The predator, the lined shore crab *Pachygrapsus crassipes*, has been previously reported to feed mainly on algae and diatoms, and on detritus and carrion when available. It occasionally eats living prey including limpets, snails, hermit crabs, and flies (Garth and Abbott 1980).

P. crassipes predation on *S. purpuratus* was observed on two separate occasions, both of which coincided with June spring tides and exceptionally calm swell conditions. On these occasions the crabs moved down from the high intertidal zone into low intertidal zone tidepools that were densely carpeted with urchins in bowl-shaped burrows. The crabs removed the urchins from their depressions by clipping the urchin's spines with their chelae until they could roll the urchins out of the depressions. Once the urchins were removed, the crabs turned them over, broke into the test through the mouth region, and fed on the internal organs (Figs. 1, 2).

During one low tide period eight to ten crabs removed and ate approximately 20 to 30 urchins, completely clearing a tidepool. Had there been a swell the tidepool would have been periodically awash and it is doubtful that the crabs

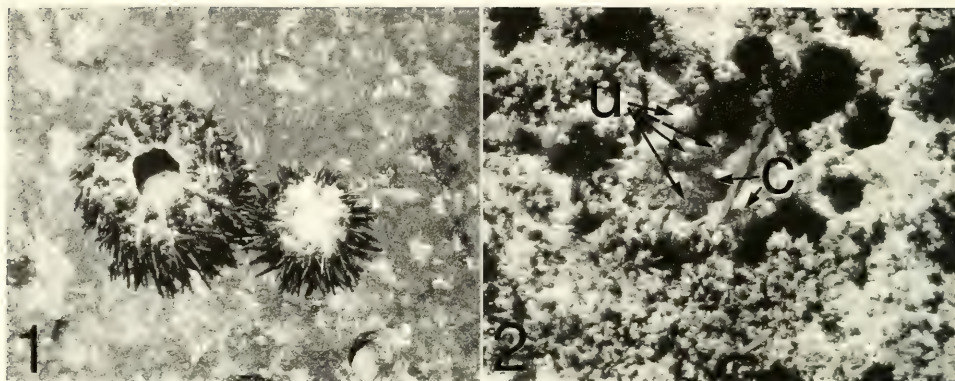


Fig. 1. *Strongylocentrotus purpuratus* preyed upon by *Pachygrapsus crassipes* on San Nicolas Island, California, June 1981. Note clipped spines on sides towards top of picture.

Fig. 2. *Pachygrapsus crassipes* feeding on *S. purpuratus* *in situ*. u = urchins, c = crabs.

Photographs reproduced from 35 mm Ektachrome slides.

would have had such easy access to the urchins. On the second occasion, two crabs were found with the remains of five urchins in a tidepool. The former tidepool has remained urchin-free for the past two years, and coralline algae (*Corallina vancouveriensis*) now covers most of the depressions that were formerly occupied by urchins.

In a related incident, M. G. Kellogg (pers. comm.) has observed the rock crab (*Cancer antennarius*) clipping spines and denuding portions of the test of *S. purpuratus* in tidepools on Southeast Farallon Island, San Francisco County, California (37°42'N, 123°00'W). Once the spines were clipped the crab broke through the denuded portion of the test with its claws and ate the urchin.

As Estes, Jameson, and Rhode (1982) and others have pointed out, biologists seldom observe predation, just its results. The presence of numerous, unoccupied urchin burrows is a common sight at many rocky intertidal areas. Typically, the absence of urchins from these habitats where they once occurred is thought to have resulted from human predation or possibly from disease. While there is little doubt that human predation does account for much of the loss, the lined shore crab *Pachygrapsus crassipes* and possibly other brachyuran species are capable of producing the identical pattern and therefore should also be considered.

Acknowledgments

I wish to thank D. L. Lindberg for field assistance, the U.S. Naval Pacific Missile Test Range (especially R. Dow) for access to San Nicolas, and J. S. Pearse for commenting on the manuscript. This work was supported by the U.S. Fish and Wildlife Service.

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Accepted for publication 30 March 1984.

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COVER: Female cheetah (*Acininyx jubatus*) and young, resting on the Serengeti Plains, Tanzania.
Photograph by Gretchen Sibley, Managing Editor.